

Some Relationships between Mammal Hosts and their Ectoparasites

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The principal objective of the Panama survey was to collect, record, and/or describe the blood-sucking ectoparasites of mammals and, to a much lesser extent, of birds and reptiles. Similarly, it was intended originally that this volume would serve primarily to delineate this fauna so that investigators of systematics, as well as of zoonoses and epidemiology, would have a firm taxonomic basis for future studies.

However, after reviewing all the papers, we felt it desirable to briefly consider some implications of the data concerning relationships of the hosts and their parasites. These relate chiefly to host-specificity, some epidemiological aspects of host specificity and ecology, altitudinal distribution, and faunal relationships and their zoogeographic implications. Because the objectives of the survey were limited, most of the data were not gathered or recorded with these problems in mind. Nevertheless, the data did provide some insight, and in a few cases suggested possible answers. The data available for bird and reptile hosts and their parasites in Panama are so limited that we have given them little consideration in the following discussion.

I. Host Specificity

Mayr (1957) has raised a number of interesting questions about the problems and implications of host-parasite specificity, for instance (op. cit., p. 8) :

"Where does host specificity occur?—How strict is it?—What groups of parasites are most host specific?—Why are some parasites highly specific, others of rather wide distribution? . . . The answers to these questions in the literature appear

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to be largely of the 'example' type. We learn that cestodes and mallophaga tend to be highly host specific, acanthocephalans and some fleas less so. It seems to me that enough information is now available to permit a more statistical approach. Statistics of reliability in the host specificity of the parasites are highly important in order to judge the value of parasites as indicators of relationship in all those special cases where the student of vertebrates is still undecided on the classification of his material."

Mayr was primarily concerned with problems such as the parallel evolution of host and parasite, and of zoogeography. These are intimately related to the ecology of both hosts and their parasites. Consequently, the questions he asked are fundamental to the whole gamut of parasite population problems, including the ecology of parasitization, and thus to the practical problems of epidemiology as well.

Mayr's statement concerning the need for statistics of reliability in host specificity is well founded, but in the case of ectoparasites, we do not agree with him that "enough information is now available to permit a more statistical approach." Excluding a few groups and certain limited geographic areas, the published host records of ectoparasites are quantitatively scanty and unevaluated. The associations themselves are often dubious, chiefly because of inadequate sampling techniques or unreliable identifications. Most of the older collections were made by vertebrate zoologists. Because they were overburdened with collecting and with preparing skins, they could rarely live-trap the hosts, keep them separate, or anesthetize them before searching for parasites. Nor could they examine more than a small number of those collected. Many of the ectoparasites were taken from the skinning table as they were noticed, or when it was convenient.

Nevertheless, these collections were of great importance. Often, they were from hosts and areas not previously represented in collections. They form the core of what is known about tropical ectoparasites. Such collections will continue to be important in filling the great faunistic gaps that still exist. But the quantitative and qualitative data that are needed to establish host relationships on a statistical basis have rarely been gathered, except in autecological studies. These studies are of great importance, but are usually scattered and do not relate the parasite populations to those of other hosts, or of other geographic areas.

The experience gained in studying and evaluating the results of the Panama survey, indicates that in order to meaningfully explore the kinds of problems discussed below, far more refined field sampling techniques, new kinds of field data, and new methods of recording and analyzing them are needed. Sampling must be carefully controlled, intensive, and representative (geographically, seasonally, and in terms of hosts). The data must be recorded in such a way that they can be machine or computer-processed. The volume of data obtained in an extensive survey, as in Panama, cannot possibly be satisfactorily analyzed by exclusively empirical methods. Further, field data from various surveys should be centralized so that new information can be added and corrections made, establishing an integrated and broad basis for future analyses. Urgently needed is the devising of relatively simple statistical techniques which give reliable indices of host-parasite association and which take into account the size of the samples,

so that they can be compared with other samples (see Wenzel, Tipton, and Kiewlicz, this volume, pp. 638-643).

However, the available data do reveal certain patterns in regard to host specificity of ectoparasites of warm-blooded terrestrial vertebrates. As with parasites in general, there appears to be an evolutionary trend toward greater host specificity, with a correspondingly closer ontogenetic, morphological, and physiological adjustment to the host by the parasite. Ultimately, the host becomes the "habitat", as the parasites adapt to restricted niches on the host. Presumably, the more specialized (adapted) the parasite becomes in relation to a host, the less competition is encountered by it for that habitat or niche.

The warm-blooded vertebrates whose ectoparasites exhibit the highest degree of niche specialization and of host specificity appear to be the birds and bats. This specificity may be characteristic of any taxonomic level from family to subspecies of parasite. This is probably correlated in part with the relative ecological isolation of birds and bats and their parasites, as compared with non-flying mammals, as well their great age. Among the insect ectoparasites of bats, specificity at the family level (of the parasites) is well marked. Families that are restricted to bats include the Streblidae and Nycteriidae (Diptera), Polyctenidae (Hemiptera), Ischnopsyllidae (fleas) and Arixeniidae (Dermaptera). Of the mites that parasitize bats, the families Spelaorhynchidae and Spinturnicidae, among others, are also restricted to them. Even in such widespread trombiculid genera as *Euschoengastia* and *Trombicula*, whose larvae are temporary parasites, the species that occur on bats appear to be restricted to them.

On these hosts, ectoparasites have not only achieved a high degree of host specificity, but, in adjusting to niches on the host's body, they have undergone secondary adaptive radiation and then have speciated again along host lines. Thus the faunule of a given family of ectoparasites on a host may include a series of genera (reflecting niche adaptations), each represented on related hosts by alloxenos species which are ecological homologues (see below). This is especially marked in the biting lice (Mallophaga) of birds. In birds, the body cover is more differentiated than it is in mammals, and provides numerous niches to which parasites can adapt (Clay, 1949, 1957; Ward, 1957). To a lesser extent, this kind of niche specialization is also found in the parasites of bats (see Wenzel, Tipton, and Kiewlicz, this volume, p. 405).

This type of evolution, as Mayr (op. cit., p. 7) pointed out, implies great antiquity of association between the hosts and their parasites. But this is more than a question of time. It seems to us that such a high degree of specialization and host specificity would usually require that throughout its life cycle (or nearly so) the ectoparasite be closely associated with the host. The hazards of host finding are thus greatly reduced. It hardly seems accidental that the groups which exhibit the highest degree of host specificity are those which are host-limited³ or nearly so, that is, those whose

³ See Wenzel, Tipton, and Kiewlicz, this volume, p. 637.

life cycle is spent on the host, or whose free-living, immature stages are shortened or eliminated through ovoviviparity. This latter condition exists in nearly all ectoparasites of bats. In the pupiparous Streblidae and Nycteribiidae, ovoviviparity not only keeps the flies closely associated with a relatively mobile host, but also eliminates the dependence of the larvae on a separate source of food. Thus, the vulnerable early stages are less subject to the selective rigors of the host and non-host environments than they would otherwise be. On the other hand, little host specificity is found among those ticks whose eggs are dropped more or less at random and whose young begin their existence as "free-living" forms, dependent upon polyxeny to reduce the hazards of host-finding.

Homozygosity for many characters, including host specificity, would probably be achieved more quickly in host-limited parasites. To a greater extent, dispersal and mating of the parasites would be "vertical". That is, much of the dispersal to new host animals would be to offspring and siblings of the host; consequently, there would be more inbreeding demes among these parasites than among those, like many ticks and fleas,⁴ which exhibit little host limitation. In these there would be more horizontal dispersal, i.e., between extra-family hosts and there would be more outbreeding among the parasites. Under such circumstances, homozygosity for host specificity might be achieved more slowly, if at all. Indeed, if flexibility for host specificity proved to be necessary or advantageous (see below) there would probably be selection for either broad adaptive variability or balanced polymorphism (see below). Strict host specificity, in such groups, would be uncommon, as it appears to be in fleas. Carson's (1957) concept of homo-versus heteroselection seems to apply to populations of host-limited and non-host-limited parasites, respectively.

Fleas are the only large group of holometabolous ectoparasites whose pre-adult stages are free-living. These live in the nest, or on the ground around the home of the host. Most fleas are parasites of small mammals, especially rodents. Many of these exhibit strong territoriality and nest in small colonies. Some do not form nests, or nest singly except at breeding time, which usually fluctuates seasonally, especially in the temperate zone. Because most fleas are temperate⁵ in distribution, either latitudinally or altitudinally, the seasonal fluctuations in breeding cycles of the hosts undoubtedly play an important role in the evolution of the flea.

⁴ However, some fleas may be essentially host-limited through other mechanisms as, e.g., the ecology of the host. Fleas like *Meringis*, whose early stages take place in the deep underground nests of kangaroo rats (*Dipodomys*) in xeric areas are not only kept in close association with their host, but are correspondingly isolated from other potential hosts. The species exhibit a high degree of host specificity.

⁵ Relatively few species of mammals in the tropical lowlands have surface nests or "homes" that are suitable breeding places for fleas, perhaps because of heavy rains and flooding. Further, the majority of fleas parasitize rodents, and there are fewer species of rodents in the lowland tropics than in temperate altitudes and latitudes. Of 35 species of native fleas collected in Panama, only 12 were taken below 2000 feet, six of them from rodents, while 24 were taken above 5000 feet, 18 of them from rodents.

Hopkins (1957a) has given an interesting discussion of host specificity in fleas, and the probable role of polyhaematophagy in their dispersal and host-finding. However, as he pointed out, adequate data on host specificity are available for only a few species. In general, it seems that the probabilities of finding a suitable host or a specific host would be greatly increased if: 1), the blood of more than one host could be utilized by a flea species, at least for nourishment, if not for maturation of eggs; or 2), if several other hosts could provide the nutritional requirements for maturation of the flea ova, even though not as effectively as the "most suitable" host. The latter⁶ would in many instances probably be the one usually considered to be the "normal", "true", or "primary" host. In some instances, it would be an essential host. Such polyhaematophagy would greatly increase the chances for survival and maintenance of the species. Thus, it appears to us that some animals may be utilized primarily as "dispersal", "carrier", or "sustaining" hosts.

While some fleas appear to be promiscuous as regards hosts (Hopkins, op. cit.), it would be a mistake to assume that this is generally true and that host specificity is relatively unimportant. As noted above, a general evolutionary trend appears to be toward narrower host restriction with the host ultimately becoming the "habitat" or nearly so. We believe this to be generally true for fleas, and with the same evolutionary advantages. Adaptations to unique characteristics of a host or hosts would lessen competition from other parasites not so adapted. We agree with Hopkins (op. cit.) that most fleas have "true" or optimal hosts. These are not necessarily "original" hosts (*sensu* Holland, 1964) and may differ within the geographic range of the parasite.

In Panama, flea species of the genera *Rhopalopsyllus* and *Adoratopsylla* were taken on a number of hosts but most individuals were recorded from relatively few (table 13), and most showed a high incidence of parasitization on only one host. Cases like that of *Spilopsylla cuniculi* (Mead-Briggs and Rudge, 1960), in which maturation of ova appears to depend upon a specific blood factor of the pregnant female host (rabbit) may prove to be unusual. However, it would be surprising if blood factors of different hosts did not vary greatly in relation to the fecundity of given species of fleas and if there were not, in turn, adjustments of the fleas to these differences.

As inferred by Hopkins, polyhaematophagy would seem to be an adaptive device which permits a non-host-limited blood-sucking ectoparasite to exploit the competitive advantage of at least some degree of host specificity without overly suffering the evolutionary consequences of having free-living young. We further suggest that "horizontal" dispersal is essential to the maintenance of the heterozygosity necessary for polyhaematophagy.⁷

⁶ Caullery (1952, p. 175) has cautioned that, "The normal host in nature is not, however, necessarily that on which the parasite develops most actively. . . . animals on which pathogenic species cause acute infections are exceptional hosts . . ."

⁷ Lewontin (1959, p. 398), states, "While stable polymorphic systems arise only through the operation of interpopulational selection, the selective forces within a population tend always to a destruction of the system with a consequent return to the homozygous state."

It seems very probable that the kind of flexible host specificity or polyhaematophagy that exists in many fleas depends on balanced polymorphism. There is probably feed-back, with polyhaematophagy dependent upon horizontal dispersal, and its concomitantly greater outbreeding and heterozygosity, and heterozygosity in turn dependent upon polyhaematophagy and horizontal dispersal. Further, heterozygosity for many other characters is probably essential to a parasite species whose young and adults are exposed to a wide gamut of extra-host environmental factors. Thus, the kind of "host transfers" which occur among fleas that otherwise are relatively host-group specific may be understood (see Johnson and Layne, 1961, and "Faunal Relationships", below). This is unlike the usual situation in Anoplura and Mallophaga. These host-limited parasites have achieved a much more narrowly limited steady state (homeostasis) as regards adjustments to both hosts and extra-host environment.

II. Coexistence and Competitive Displacement⁸

The preceding discussion is based on the premise that adjustment to specific hosts and, further, to niches on these hosts, is selected for in the evolutionary process of achieving "optimal conditions of existence and survival (homeostasis)" (Emerson, 1960, pp. 342-343; see also Emerson, 1954), through lessening of competition. DeBach (1966, p. 204) has summarized this view in somewhat different terms, "Niche differentiation and habitat differentiation may be closely related aspects of the same tendency to evolve away from direct competition, and evolution of both niche and habitat differentiation permits many species to live together in communities."⁹

DeBach (op. cit.) has given an excellent review of the problems of coexistence and competitive displacement and of the pertinent literature. We agree with him (op. cit., pp. 186-190) that competition must be viewed in a broad sense, and it does not necessarily involve limited resources such as food. We agree with him further (op. cit., p. 200), that "the processes involved in competition between ecological homologues¹⁰ may be many and varied, or may not be more different from those involved in intra-specific competition with either species alone."

Whatever the processes, if the premise stated is sound, we should find

⁸ Competitive displacement is defined by DeBach (1966, p. 187) as "elimination, in a given habitat, of one species by another species where one possesses the identical ecological niche of the other."

⁹ Ward (1957, p. 458), in studying Mallophaga of birds of the genus *Tinamus* (Tinamiformes) has attributed a positive statistical association between pairs of species on these hosts to a "possible cooperative interaction between species and a diversity of the habitat which permits several species to coexist in a limited microgeographic area." We believe that his analysis of the interspecific associations of pairs of species of Mallophaga can be interpreted in terms of selective advantage without implying a cooperative interaction.

¹⁰ DeBach (op. cit., p. 186) defines "ecological homologues" as "two or more different species having the same ecological niche." They need not be taxonomically related.

evidence of coexistence and competitive displacement among ectoparasites. Such evidence could be of several types, including: observed evolutionary end results; analyses of population interactions through field sampling and/or observation; and experimental manipulation. The first type of evidence has been discussed for several groups of ectoparasites, notably the bird lice (Clay, 1957; Ward, 1957), and fleas and sucking lice (Hopkins, 1957, a,b). Analyses like these are immensely valuable in recognizing, understanding, and defining the problems, and lead to evidence of the other two types mentioned above. Unfortunately, there are few studies or papers that deal with evidence of the second type for ectoparasites. The host, habitat, and geographic distributions of two synoxenous species of the genus *Strebla* (batflies) which parasitize bats of the genus *Phyllostomus* appear to provide some evidence of these population interactions.

Throughout its range in South America and Panama, *Phyllostomus hastatus* harbors a streblid faunule consisting of a minute brachypterous, mite-like species of the genus *Mastoptera*; a fully winged, rather generalized streblid of the genus *Trichobius* (*longipes*); and one or two species of *Strebla*.

The species of *Strebla* are highly modified, polyetenoid forms, with short legs, a well-developed head ctenidium, highly modified palpi, and mouthparts with short labella. Their depressed form and short legs fit them admirably for rapid movement on the wing membranes, as well as through the pelage. They are all quite similar, though some have shorter and broader heads, or differ in other relatively minor details. The uniformity of their structure suggests that the species are ecological homologues, or nearly so. With few exceptions, they are monoxenous and alloxenous.¹¹ Two species, *S. hertigi* and *S. mirabilis*, may be synoxenous on *Phyllostomus h. panamensis*. The host relationships are shown diagrammatically in fig. 147, which should be referred to in the following discussion.

Phyllostomus h. panamensis is parasitized by *Strebla mirabilis* in Panama, Colombia, and possibly farther south, along the west coast of South America. It is also parasitized by *S. hertigi* in Panama, and possibly in Colombia, although our samples from Colombia are not extensive enough to demonstrate this. We have no collections from the west coast of South America. *Phyllostomus h. hastatus*, on the other hand—as represented in our material from eastern Venezuela, Trinidad, Surinam and Amazonian Peru—is parasitized only by *S. consocius*, a fly which appears to be monoxenous. Since *P. discolor* and its parasite *S. hertigi* are distributed throughout the range of *Phyllostomus hastatus* and beyond, it is interesting that *hertigi* coexists with another species of *Strebla* on *P. hastatus* only in part of the range of one subspecies (*panamensis*) of that host.

As noted, *hertigi* appears to be the only species of *Strebla* that parasitizes *Phyllostomus discolor*. This bat is ecologically much more restricted

¹¹ "Alloxenous" is defined in the preceding paper (p. 637) as referring to species of the same genus which occur on different hosts, as opposed to "synoxenous" (together, on the same host).

than *P. hastatus*. It is essentially a fruit-eating species that lives in groves and forests. The omnivorous and ecologically more tolerant *P. hastatus* occurs in these habitats too, but also roosts in sites like caves, tree holes, and houses. Interestingly, if one examines some of the data (table 11) for Panamanian collections, it appears that while 76 to 100% of the individuals of *P. h. panamensis* are parasitized by *Strebla mirabilis*, only 4.26 to 14.38% are parasitized by *Strebla hertigi*. If one takes into account the numbers

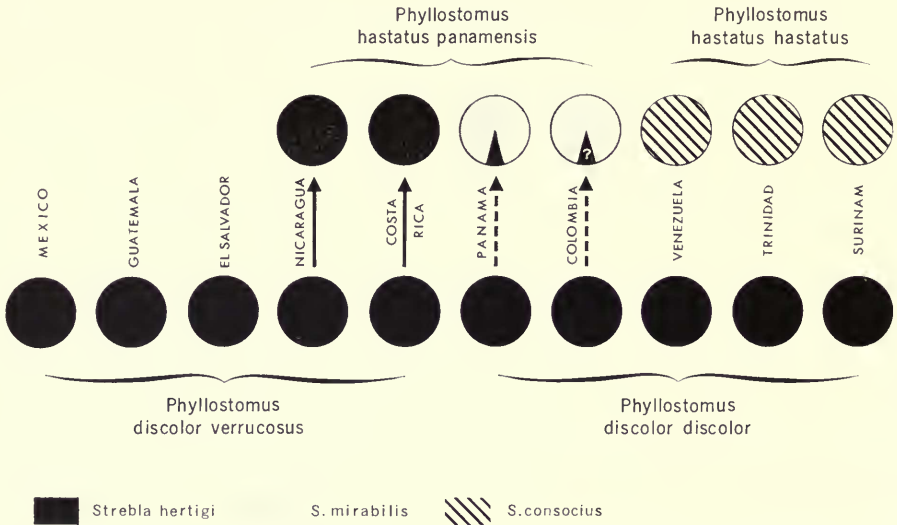


Fig. 147. Occurrence of species of *Strebla* on *Phyllostomus hastatus* and *Phyllostomus discolor* in Central America and northern South America, based on collections studied.

of individuals of the two flies, the difference is even more striking. It will also be noted (table 11) that *hertigi* was absent or nearly so, from those colonies of *P. h. panamensis* that roosted in non-forest sites like caves and buildings. This suggests that this bat is a suitable host for *hertigi* only where ecological conditions of its roosting sites are similar to those of *P. discolor*. It further suggests that *P. h. panamensis* acquires *hertigi* in those situations where it can come into contact with *discolor* and/or its parasites, probably through roosting sites. From table 11 it will be seen that in the cases cited for Panama, the mean number of *Strebla* per host bat examined (column D) ranged from 7.7 to 15.4 for *mirabilis* and 0 to 2.5 for *hertigi*. If the mean number per bat is calculated for only those bats parasitized by each species (column E) the highest for *hertigi* is 2.85. It will be noted that the highest (mean) number of *mirabilis* per bat were taken from hosts on which no *hertigi* were found.

In Costa Rica and Nicaragua, where *P. h. panamensis* reaches the northern limit of its distribution, the picture appears to be very different. Here,

TABLE 11. NUMBERS OF *STREBLA MIRABILIS* AND *S. HERTIGI* FROM *PHYLLOSTOMUS H. PANAMENSIS*.
(Central America)

Localities	A Hosts parasitized by Streblidae/ number examined.	B Percentage of host bats parasitized: <i>mirabilis hertigi</i>	C No. of <i>Strebla</i> collected:		D Mean no. per bat from <i>panamensis</i> examined:		E Mean no. of <i>mirabilis</i> or <i>hertigi</i> per bat parasitized by each:	
			<i>mirabilis</i>	<i>hertigi</i>	<i>mirabilis</i>	<i>hertigi</i>	<i>mirabilis</i>	<i>hertigi</i>
PANAMA								
Chepo Road (Panamá) (Hollow tree in forest)	16/16	100.00	200	40	12.50	2.50	12.50	2.85
Chilibrillo Caves (Panamá)	16/17	76.57	206	1	12.11	0.06	12.87	1.00
Madden Dam (Canal Zone) (Natural bridge and small cave)	13/14	92.85	170	2	12.13	0.14	13.07	1.00
Fort Kobbe (Canal Zone) (Hollow <i>Ficus</i> tree)	5/5	100.00	77	0	15.40	0.00	15.40	0.00
Fort Sherman (Canal Zone) (Buildings & bunkers)	19/19	100.00	146	1	7.68	0.53	7.68	1.00
COSTA RICA								
All localities (3)	10/11	0.00	0	38	0.00	3.45	0.00	3.80
NICARAGUA								
NE of Condega (Estelí)	6/6	0.00	0	39	0.00	6.50	0.00	9.74

none of the specimens collected were parasitized by *S. mirabilis*! The only species of *Strebla* present on that host was *hertigi*. All of the six host bats included in the sample from Nicaragua were parasitized by Streblidae, but only four (66%) by *Strebla hertigi*. On these four bats (column E), the number of *hertigi* per bat was 9.74! Thus, when *mirabilis* was absent, the numbers of *hertigi* per bat increased to a level nearly comparable to those of *mirabilis* on *P. h. panamensis* in Panama.

We are not certain that *Strebla mirabilis* is absent from *P. h. panamensis* throughout Costa Rica and Nicaragua. Interestingly, a single collection from Sibube (Bocas del Toro), Panamá (near Costa Rica) had three specimens of *hertigi* and two of *mirabilis*. One individual of *P. h. panamensis* from Armila (San Blas), had five *hertigi* and no other Streblidae.

Why is *S. mirabilis* replaced by *hertigi* on *Phyllostomus h. panamensis* in Costa Rica and Nicaragua? Several answers may be suggested. The simplest is that toward the northern limit of its range, the roosting sites and/or population structure of the host are not as suitable for *Strebla mirabilis* as they are further south, nearer the epicenter of the host's range,¹² and thus *mirabilis* cannot maintain itself on this bat at these latitudes. Another possibility, which assumes that *Phyllostomus discolor* is the "reservoir" of the *hertigi* that parasitize *P. h. panamensis*, is that the *hertigi* on *P. discolor discolor* differ from those on *P. discolor verrucosus*.¹³ If this is so, it may be that the population on *P. discolor discolor* is better adapted to *P. h. panamensis* than is *S. mirabilis*, and thus competitively displaces *mirabilis* on that host in Costa Rica and Nicaragua. The differences in the *Strebla* populations on *P. h. panamensis* do appear to coincide with the geographic separation of the two races of *P. discolor* (fig. 147). However, if the single small collection from *P. h. panamensis* taken at Sibube is indicative, then there may be a geographic gradient in the ratio of *mirabilis* to *hertigi* on that host. This would lend support to the first explanation. Unfortunately, nearly all of the Panamanian collections are from the Canal Zone and the Province of Panamá. Extensive intermediate collections are necessary for an understanding of this problem.

Whatever the explanation, the salient fact is that in Panama—where the two species of *Strebla* coexist on the same host—the mean number of *hertigi* per host is very small compared with that on its normal host, and with that on *P. h. panamensis* in Costa Rica and Nicaragua where it does not coexist with *mirabilis*. These data strongly suggest that in Panama some kind of competitive interaction between *hertigi* and *mirabilis* keeps the population of *hertigi* on *P. h. panamensis* at a lower level than when *mirabilis* is absent. They further suggest that *mirabilis* is absent from this host in Costa Rica and Nicaragua because of competitive displacement.

¹² One could similarly argue that at these latitudes climatic or other ecological conditions are not suitable for *mirabilis*, though the occurrence of this species even farther north at higher elevations, on *Trachops cirrhosus* is then difficult to explain (see p. 617).

¹³ We are unable to detect morphological differences between specimens of *hertigi* from these two subspecies.

If this is so, it may also explain the failure of either *hertigi* or *mirabilis* to parasitize *P. h. hastatus* in the presence of *S. consocius* (fig. 147). However, one can also argue that this host is physiologically or ecologically (specifically?) so distinct as to be unsuitable for either *hertigi* or *mirabilis*, even though *mirabilis* is present on *Trachops*,¹⁴ and *hertigi* on *Phyllostomus d. discolor* in areas occupied by *P. h. hastatus*.

"Delousing" the hosts and infesting them with known numbers of parasites may provide evidence of the third type, i.e., the evidence derived through experimental manipulation. The host bats are easily kept alive in the laboratory (See Wenzel, Tipton, and Kiewlicz, p. 425, this volume).

Barnes (1965, pp. 274-276) has suggested that two California fleas of the genus *Anomiopsyllus* which live in the nests of the wood rat, *Neotoma fuscipes* are mutually exclusive (competitive displacement, *sensu* DeBach, op. cit.). A rather similar host distribution was noted by Tipton and Méndez (pp. 317-318, this volume) for *Kohlsia mojica* and *traubi* (and perhaps *keenani*) on *Peromyscus n. nudipes* in Panama. While some differences in geographic and ecological distribution appear to be involved, these may be factors in the process of competitive displacement (see DeBach, op. cit. p. 204).

Complementary distributions on quite a different taxonomic level, may also bear analysis in this connection, for example: the world-wide host and geographic distributions of Streblidae and Nycteribiidae; the relative absence of Streblidae and Nycteribiidae on Molossidae, which are parasitized by Polyctenidae; or the absence of dermanyssid mites on oryzomyine rodent hosts, which are normally heavily parasitized by laelaptid mites of the genus *Gigantolaelaps* (see Yunker and Strandtmann, this volume, p. 83).

III. Epidemiological Considerations

Of approximately 212 terrestrial mammals reported for Panama (including man and 10 introduced species), ectoparasites are recorded for 155. Undoubtedly many more species occur than are indicated in the comprehensive host-parasite list (p. 797). The collections here reported were not made with statistical analysis in mind, and thus were not uniform in sampling, recording techniques, or in coverage. For example, relatively few collections of ectoparasites were made in the subtropical zone (approx. 2500-5000 feet). Because of this, we have had to carefully select our data in treating various aspects of host-parasite relationships. Nonetheless, with these and other factors taken into account, it is evident that certain hosts acquire a disproportionately large number of parasites in comparison with others.

Large numbers of species of ectoparasites were recorded for certain *euxenous* (= hospitable) hosts, as opposed to *apoxenous* (= inhospitable) hosts, which had few or none (fig. 148). For example, 15 or more species of ectoparasites were reported from 18 host species: 41 from the opossum,

¹⁴ See Wenzel, Tipton, and Kiewlicz (p. 617, this volume) for a discussion of the taxonomic status of "*mirabilis*" on *Trachops*.

Didelphis marsupialis; 37 from the spiny rat, *Proechimys semispinosus*; 31 from the short-tailed bat, *Carollia perspicillata azteca*; 29 each from the spiny pocket mouse, *Heteromys desmarestianus* and the deer mouse, *Peromyscus n. nudipes*; 25 from the cotton rat, *Sigmodon hispidus*; 24 each from the tree squirrel, *Sciurus granatensis*, and the coati, *Nasua nasua*; 23 each from the rice rat, *Oryzomys capito* and the cane rat, *Zygodontomys microtinus*; 21 from *Homo sapiens*; 19 each from the porcupine rat, *Hop-*

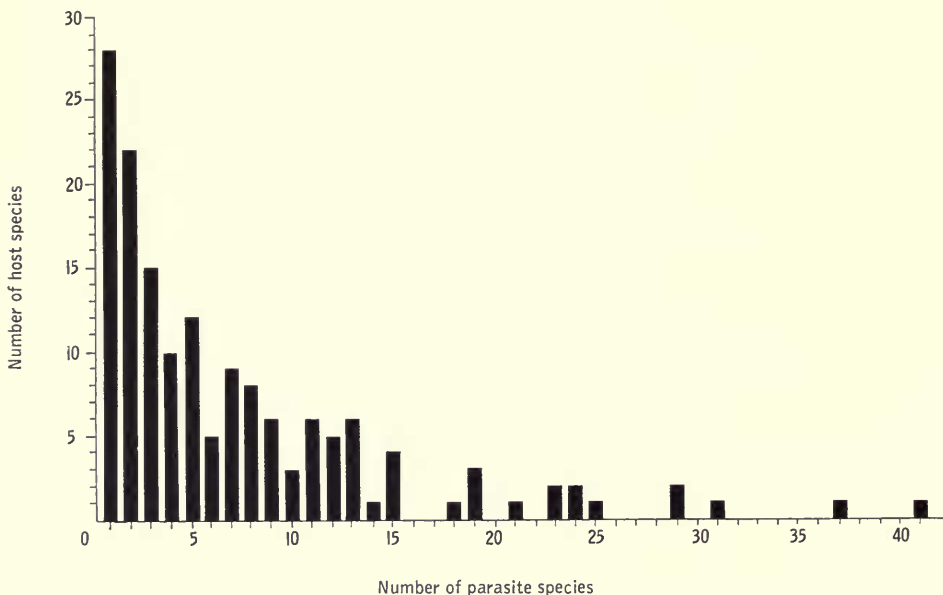


Fig. 148. Numbers of species of mammal hosts, according to numbers of species of ectoparasites taken from each in Panama. Negative hosts are not included.

lomys gymnurus, the spiny pocket mouse, *Liomys adspersus*, and the rice rat, *Oryzomys caliginosus*; 18 from the four-eyed opossum, *Philander opossum*, and 15 each from the brown mouse, *Scotinomys xerampelinus*, the nine-banded armadillo, *Dasypus novemcinctus*, and the fruit bat, *Artibeus j. jamaicensis*. In general, analysis of the other hosts indicates that the number of nonspecific (exceptional) parasites decreases with increasing ecological specialization and/or geographical restriction of the host.

The species with the largest number of parasites reported for it is the common opossum, *Didelphis marsupialis*. Of 41 species reported for this host from Panama, probably no more than four or five are characteristic parasites and none appear to be monoxenous! Four are characteristic parasites of marsupials, but not of *Didelphis* alone. These are a dermanyssid mite, *Ornithonyssus wernecki*; a tick, *Ixodes luciae*; and a flea, *Adoratopsylla i. cophi*; the fourth is a flea, *Juxtapulex echidnophagoides*, which occurs on both marsupials and the armadillo, *Dasypus novemcinctus*, in Panama. It

appears then, that *Didelphis* must acquire most of its parasites from other hosts. It is a truly ubiquitous, ecologically broadly tolerant animal, which ranges from sea level to above 5000 feet elevation, in Panama.

It moves through and between a number of ecological formations, both horizontally and altitudinally, and thus comes into contact with many other components of the communities of which it is a part, including other hosts and their parasites. Some of these parasites move onto *Didelphis*, in varying degrees of association, mostly in small numbers, as opportunity permits or circumstances require. An individual opossum carries a much smaller number of species than is apparent from the comprehensive host-parasite list, the faunule varying from habitat to habitat, and especially at different elevations.

The fleas reported from *Didelphis* illustrate this point (see Tipton and Méndez, this volume, p. 326). Below 2500 feet, they were: an agouti flea, *Rhopalopsyllus a. tupinus*; a paca flea, *R. l. lugubris*; an armadillo flea, *R. cacticus saevus* (probably through use of armadillo burrows); and *Polygenis klagesi*, from the ubiquitous spiny rat, *Proechimys semispinosus*. Between 2500 and 5000 feet elevation, they were *Polygenis r. beebei* (from species of *Oryzomys*, especially *O. caliginosus* and *O. capito*); and the marsupial flea *Adoratopsylla i. copha*. At elevations above 5000 feet, they were: the rabbit flea, *Hoplopsyllus glacialis exoticus*; *Juxtapulex echidnophagoides*, shared by *Didelphis* and the nine-banded armadillo; a squirrel flea, *Pleochaetis d. dolens*; and more abundantly than at lower elevations, a marsupial flea, *Adoratopsylla i. copha*. Throughout its range, *Didelphis* was occasionally parasitized by the cat flea, *Ctenocephalides f. felis*. This kind of pattern is reflected in the other groups of ectoparasites collected from the opossum, too.

While its ecological tolerance and vagility obviously influence the number of parasites it acquires, *Didelphis* may tolerate a greater variety of parasites than do many other hosts. It is a primitive animal that is only superficially specialized. Many parasites adjust to specialized differences of the hosts. It is significant that so many parasites of New World marsupials show little specificity to host species, but rather to marsupials as a group. The large number of ectoparasites it acquires may partly reflect an easier "penetration" of *Didelphis* by non-specific parasites, due to the relative absence of competition from forms which are more narrowly adjusted to it or from forms which may be adjusted to it only in certain environments.

The interrelationships between *Didelphis* and other hosts are far more numerous and complex than indicated by the above discussion. In Panama more than 70 hosts were recorded for the 37 non-marsupial parasites that were reported from *Didelphis*. These included 11 species of birds and reptiles and three of bats. Thus, the number of possible interrelationships through exchange of ectoparasites and/or micro-organisms, directly, or indirectly through "intermediary" hosts, is enormous.

Didelphis could well play an important role in the dissemination of ecto- and endoparasites between animals that are ecologically more restricted. This might also be true of some of the other euxenous hosts.

While there appears to be little taxonomic relationship between these "carrier" hosts, all have one feature in common with *Didelphis*, namely that they contact many components of a community, but in different ways. Among the bats, *Carollia perspicillata azteca* (see Wenzel, Tipton, and Kiewlicz, this volume, p. 638) roosts in a wide variety of sites and with a variety of hosts. Tree squirrels, on the other hand, contact a wide range of components through their foraging and nesting activities, both on the forest floor and in the tree strata.

Many of the euxenous hosts are ubiquitous in yet another sense. Some, like *Proechimys semispinosus*, *Peromyscus nudipes*, *Oryzomys capito* and *O. albigularis* may be abundant more or less uniformly distributed (pervasive) forest animals, and the grassland *Sigmodon hispidus* and *Zygodontomys* may be similarly distributed. Some of these hosts exhibit considerable sociability and even commensalism. Further, populations of such common and widespread species may be restricted to "pockets" in areas where their habitats are discontinuous. In the presence of an extraordinary abundance of food, such a population may increase far beyond the ordinary carrying capacity of the pocket. With the exhaustion of this extraordinary increment of food, the excess numbers of rodents may spill over into neighboring areas in outbreaks that are referred to as *ratadas* or "rat plagues" in rural South America.¹⁵

From the lists of ectoparasites given for them (p. 797), it is obvious that hosts like these must have contacts with many other host species or their runways, nests, etc., and/or their parasites. Further, rat plagues or *ratadas* must provide unusually favorable circumstances for exchange of both ecto- and endoparasites and other micro-organisms. It is quite likely that they may acquire pathogens from ecologically more restricted hosts and ectoparasites, and thus become "carriers" or even reservoirs, in the epidemiological sense.

Although no arthropod vectors have been demonstrated, the ecology of the Beni (Bolivia) epidemic of haemorrhagic fever emphasizes the importance of this type of host. *Proechimys guyannensis*, and *Calomys callosus*, two rodents that have been incriminated in the epidemiology of this disease (Kuns, 1964), are typical *ratadas* forms (Hershkovitz, pers. comm.). *Proechimys semispinosus* (see above) is one of the notable euxenous hosts in Panama.

For ectoparasites one could assemble a graph very similar to that (fig. 148) shown for the hosts. The largest number of host species were recorded for Acarina, especially chiggers and ticks, and a few fleas like *Ctenocephalides felis*. Brennan and Yunker (this volume, p. 235) recorded 35 hosts each for the chiggers *Eutrombicula goeldii* and *E. alfreddugesi*, in Panama. The epidemiological importance of such non-specific (promiscuous) or of

¹⁵ Hershkovitz (1962) has given an extended discussion of pocket populations and *ratadas*. He cites instances in which *ratadas* of South American cricetines are correlated with cyclic fruiting and seed production of bamboos. As many as 17-20 years may elapse between fruiting.

polyxenous ectoparasites, especially the immature stages of heteroxenous ticks, is well documented in the literature on arthropod-borne diseases.

If survey and sampling techniques are sufficiently refined, it should be possible, through modern data processing, to analyze many of the complex interrelationships between hosts, parasites, and the extra-host environment. This should not only lead to a better understanding of the population dynamics, but may make it possible to evaluate hosts and ectoparasites of a given area in terms of their potential epidemiological importance.

IV. Altitudinal distribution

In the following discussion we refer to tropical, subtropical, and montane zones in the sense of Holdridge and Budowski (see fig. 149 and Fairchild, "Introduction," p. 5, this volume). This differs from the classification of Goldman and Zetek (1926) and that of Fairchild (loc. cit.). The tropical zone of Fairchild correlates more closely with many parasite distributions than does that of Holdridge and Budowski. When we describe groups as being temperate in distribution, we are referring to their climatic adjustment without restricting them geographically.

A. Mites and Ticks

Family Laelaptidae

Subfamily LAELAPTINAE. Most of the laelaptine mites occurred in the tropical and subtropical zones. Some, like *Laelaps nuttalli* and *Echinolaelaps echidninus* (both introduced), were taken only near sea level. Others, like *Haemolaelaps glasgowi*, were taken from sea level to 7500 feet. Tipton, Altman, and Keenan (this volume, p. 34) suggest that this species is composite. Most species of *Gigantolaelaps* were tropical and subtropical, like their oryzomyine hosts. However, *G. inca* (described from Peru) was taken only above 5000 feet, as was *Eubrachylaelaps jamesoni* (described from Mexico). The native species of *Laelaps* showed considerable differences in their altitudinal ranges. Some, like *pilifer* and *dearmasi*, occurred only in the tropical and subtropical zones, while others, like *thori*, were taken between 2000 and 7800 feet.

Families Dermanyssidae, Trombiculidae

We cannot assess the altitudinal distributions of these two families. In general, the Dermanyssidae appeared to be tropical and subtropical in distribution, though *Ornithonyssus bacoti*, the Tropical Rat Mite, was taken from sea level to 5000 feet. The Tropical Fowl Mite, *O. bursa*, occurred at low elevations, while *O. sylviarum*, the Northern Fowl Mite, was taken at 5700 feet on Volcan Chiriquí, the southernmost record of this species.

Family Spinturnicidae

The altitudinal distribution of these mites was very similar to that of the Streblidae (see below). As in the case of the streblid *Joblingia*, the spinturnicid genus *Paraspsinturnix* on *Myotis n. nigricans* was taken only in the lower montane zone.

Superfamily Ixodoidea

The altitudinal distribution of the ticks is discussed by Fairchild, Kohls, and Tipton on pp. 168–170, this volume. Most species of *Amblyomma* occurred in the lowlands and those of *Ixodes* in the highlands.

B. Rove Beetles

Family Staphylinidae

The parasitic amblyopinine staphylinid beetles are primarily temperate in their distribution, both altitudinally and latitudinally in South America. The Middle American species, including those taken in Panama, are from the montane zones. The distribution shown for *Amblyopinus tiptoni* (fig. 150) is typical.

C. Batflies (Diptera)

Family Streblidae

The Streblidae are primarily tropical and subtropical in distribution, with very few species in the warm temperate and none in the cool temperate regions. This is strikingly illustrated by their altitudinal distribution in Panama. Of the 66 species recorded from Panama, 49 (ca. 75.4%) were restricted to the tropical zone, or nearly so. The ranges of a few of these extend into the lower elevations of the subtropical zone.

About nine species (12.3%) were either restricted to the subtropical zone or ranged from the tropical or subtropical zones to the lower altitudes of the lower montane. Three of these—*Anastrebla mattadeni*, *A. modestini*, and *Exastinion clovisi*—occurred only on bats of the genus *Anoura*, which are primarily subtropical. The other six species were parasites of fruit-eating bats (Phyllostomidae: subfamilies Stenoderminae and Sturnirinae).

Four species (6.2%) were taken only in the lower montane zone. These were *Joblingia schmidtii* from *Myotis n. nigricans*, *Anatrichobius scorzai* from *M. chiloensis*, *Trichobius keenani* from *Sturnira ludovici*, and *T. vampyropis* from *Vampyrops vittatus*. No species were taken in the upper montane zone.

A few species had a considerable altitudinal range. Three (4.6%) occurred with their hosts, *Desmodus r. rotundus* and *Trachops c. cirrhosus* from sea level to nearly 5600 feet. *Paratrichobius "longicrus"* showed a similar altitudinal range, but occurred on different stenodermine hosts at different elevations. It may be a composite species (see Wenzel, Tipton, and Kiewlicz, this volume, p. 519).

For the most part, the altitudinal range of a host and its Streblidae coincided closely. An outstanding exception to this is the very restricted distribution of *Joblingia schmidtii*, as compared with its host *Myotis n. nigricans*. As Handley points out (p. 770) this bat is probably a composite species. According to him (pers. comm.) the montane population is probably a separate species, while the lowland population in Panama may consist of several cryptic species. This probably explains the puzzling distribution of species of *Basilia* (Nycteribiidae) on this host in Panama and elsewhere in Latin America.

Family Nycteribiidae

Although the Nycteribiidae appear to tolerate cooler climates and penetrate further into the temperate regions than do the Streblidae, this was not reflected in the altitudinal distributions of the seven species that have been collected in Panama. All are from the tropical zone.

D. Fleas

The altitudinal distribution of the fleas is shown in figure 149. It should be emphasized that the ranges of a number of the species would be extended by further collecting and also that the chart does not reflect relative abundance at different altitudes. Although some species were taken throughout a considerable altitudinal range, they were obviously most abundant in a much narrower one. This is reflected in the data given by Tipton and Méndez (beginning on p. 325, this volume).

Family Pulicidae

Tunga penetrans is the only New World species of the genus that is not restricted to Southern Brazil (São Paulo, Bahia, Goyaz). It occurs from South America to Mexico and has a correspondingly broad altitudinal range as well (fig. 149). The known species of *Rhynchopsyllus* have the same altitudinal distribution as their host bats (genus *Molossus*). *Juxtapulex echidnophagoides*, known from Costa Rica (+4300 feet elev.), and Panama, has an altitudinal range similar to that of the batfly, *Joblingia*, as does *Hoplopsyllus glacialis exoticus*, from Panama. All of the 859 specimens of *Juxtapulex* collected in Panama were from above 5000 feet elevation. The altitudinal ranges of *Pulex irritans* and *P. simulans* are interesting. They are discussed by Tipton and Méndez (this volume, p. 293), who feel that *simulans* may be lowland and *irritans* highland in Middle America.

Family Rhopalopsyllidae

These fleas are principally South American. Most of the South American genera are decidedly temperate in distribution, but the two large genera, *Rhopalopsyllus* and *Polygenis*, are represented in the subtropical and tropical zones. Nine species of these two genera were taken in Panama. Seven were primarily tropical and subtropical in distribution and two were taken only in the lower montane.

Family Ceratophyllidae

Species of five genera were collected in Panama. *Ceratophyllus altus*, the only species of the genus known from Panama, occurs in the lower montane zone. *Dasypsyllus gallinulae perpinnatus*, another bird flea, is altitudinally and latitudinally temperate, and occurs from Western North America to Panama and probably South America (Johnson, 1957). It was taken in the lower montane zone of Panama. *Dasypsyllus l. venezuelensis* occurs in the same zone, but at slightly lower elevations. The other three genera of Ceratophyllidae that were taken in Panama are *Jellisonia*, *Pleo chaetis*, and *Kohlsia*. These three genera of rodent fleas are centered in the

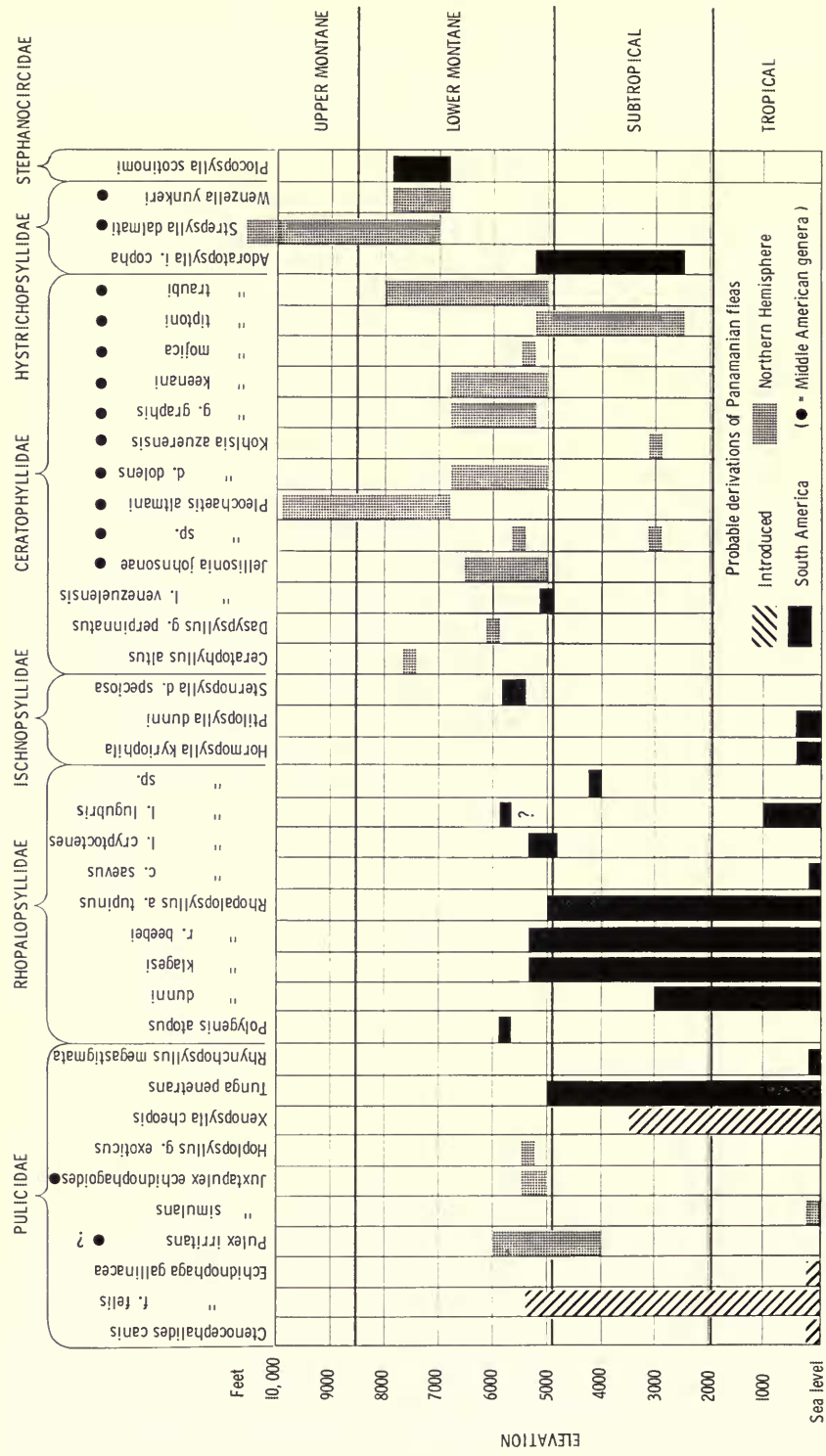


Fig. 149. Altitudinal distribution of fleas collected in Panama.

warm temperate and temperate zones of Middle America and Mexico, and this is reflected in their altitudinal distribution. A few species were taken in the subtropical, but none in the tropical zone.

Family **Ichnopsyllidae**

The bat fleas were represented by two lowland South American genera, *Hormopsylla* and *Ptilopsylla*, both of which occurred at or near sea level, and by *Sternopsylla distincta speciosa*, which occurred in the lower montane zone. *Sternopsylla* is closely related to the other two genera and occurs as *S. distincta distincta* in central and southern United States.

Family **Hystrihopsyllidae**

*Adoratopsylla i. coph*a, taken in subtropical and lower montane zones, is a South American race of a species belonging to a South American genus. It occurs in Mexico as *A. i. intermedia*. *Strepsylla dalmati* and *Wenzella yunker*i, both known only from the upper montane zone, belong to genera that are endemic to the highlands of Middle America.

Family **Stephanocircidae**

Plocopsylla scotinomi, the only known Middle American species of the temperate South American subfamily Craneopsyllinae, was taken only in the upper montane zone.

In general, ectoparasite taxa of South American relationships occurred below and those of holarctic affinities above 5000 feet elevation.

V. Altitudinal Concordance Between Hosts and Parasites

The altitudinal distributions of host-limited parasites like the Spinturnicidae and of nearly host-limited ones like the Streblidae and Nycteribiidae paralleled those of their hosts quite closely. The collections of biting and sucking lice were not adequate to determine to what extent this was true for them. It is not true of groups like the fleas, ticks, and the laelaprine mites, which in general are not host-limited. The data for the Laelaptinae must be treated with considerable caution, because some of the species may be composite (see Tipton, Altman, and Keenan, this volume, p. 31).

In figure 150, we have shown the altitudinal distribution of a series of representative mammal hosts and some of their characteristic non-host-limited parasites. The altitudinal ranges must not be taken too literally, for several reasons. First, they do not reflect the relative abundance of the hosts and parasites at different elevations. The data on altitudinal distribution of the fleas given by Tipton and Méndez (beginning on p. 325, this volume) give an indication of this, but the nature of the field data does not permit detailed analyses of this type. Second, the data are lumped for all of Panama. Regional and edaphic climatic differences greatly modify the fauna and flora and thus affect the altitudinal range of both host and parasite in a given locality, as do other environmental factors. Environments on the drier Pacific slopes of the mountains are quite different from

those on the more humid Atlantic slopes. Similarly, the habitat at the summit of a mountain 4000 feet high differs from that at the same altitude on a mountain that is 10,000 feet high. Carefully documented field collections and ecological observations should provide an appreciation of these factors.

In spite of the limitations of the data, it is clear that the altitudinal ranges shown for many parasites do not coincide with those of the hosts. Nor does the altitudinal range of a parasite on a given host necessarily coincide with the entire altitudinal range of the parasite. In some instances, as in the case of the flea *Jellisonia johnsonae* (fig. 150) these differences could reflect sampling techniques or local edaphic differences. On the other hand, the flea *Strepsylla dalmati* was taken on *Peromyscus n. nudipes* from about 5500 feet to the altitudinal limit of this host at 8000 feet; but it was taken above this altitude on other hosts, like *Reithrodontomys* and *Scotinomys*. Similarly, *Pleochaetis altmani* was taken on *Scotinomys xerampelinus* and *Reithrodontomys creper*, between 5600 and 8000 feet (fig. 150), but a few specimens were taken on *Reithrodontomys sumichrasti* at 10,300 feet.

Other authors have also indicated that parasites may not have as broad distributions as the hosts. This may be an attribute of non-host-limited forms. The population density of most hosts must decrease as one moves away from optimum habitat conditions, and the opportunities for their non-host-limited parasites to encounter a suitable host probably decrease correspondingly, or even disproportionately because of their lesser vagility. Under these circumstances, one might expect selection to narrow the ecological range of a parasite so that it corresponds more nearly to the optimal environmental conditions of the most suitable host(s). In this respect, it should be remembered that homoiothermal hosts would have relatively greater ability to move into climatically less suitable habitats than would poikilothermal non-host-limited parasites.

It must also be noted that distribution may be correlated with subspecies of the host. For example, no fleas were taken on *Sciurus granatensis* below 5000 feet. All, including those apparently specific to this host, were from the subspecies *S. granatensis chiriquensis*, above 5000 feet. Similarly, *Wenzella yunker* was taken only from *Heteromys desmarestianus chiriquensis*, but not from the other subspecies that occurred at lower elevations. It is clear that in the future, host identifications to subspecies must be given whenever possible. Correlation between host subspecies and parasites and altitudinal data may in some cases indicate that the taxonomic status of the host merits further investigation.

VI. Faunal Relationships

Few groups of ectoparasites are well enough known for the Neotropical Region as a whole to permit an evaluation of the faunal relationships of their Panamanian representatives. Though it is not well known for either Middle or South America, we believe that the flea fauna of Panama and certain other critical areas has been sampled well enough to give a general picture of the distribution of the families and genera. Very large and representative collections of batflies (chiefly Streblidae) are at hand from Middle

America, and representative samples have been secured from northern South America and to some extent Peru, though the fauna of the Amazon basin is still largely unknown. The distribution of the amblyopinine beetles (Staphylinidae) and the laelaptine mites also contribute some interesting points that bear on faunistics and zoogeography.

In the following discussion we refer to all of the North American continent between the northern boundary of Mexico and the southern boundary of Panama as Middle America, and to the area north of Mexico as North America. We have arbitrarily used the term in this geographic sense as did Baker (1963), rather than in a zoogeographic sense (see Hershkovitz, 1958). However, we have followed Hershkovitz (op. cit.) in his use and definition of the Patagonian Subregion.

In the following discussion, it should be remembered that of 50 genera and \pm 300 species of cricetine rodents recorded from South America, all but two recent invaders (see Hershkovitz, this volume, p. 738) are complex penis types and no parasites have been reported for these two. Thus, when we refer to South American complex-penis-type Cricetinae, we do not infer that there are South American simple-penis-type hosts for which ectoparasites have been reported. Both groups are well represented in Middle America.

A. Mites

Family Laelaptidae

Subfamily LAELAPTINAE. The geographic and host distribution of the laelaptine mites are instructive. Eight genera were taken from rodents in Panama. Four of them belong to a complex of six closely related genera (Tipton, 1960, p. 258). These are *Laelaps*, *Tur*, *Mysolaelaps*, and *Echinolaelaps*. *Laelaps* and *Echinolaelaps* are cosmopolitan and occur mostly on Murinae, Microtinae and complex-penis-type Cricetinae. They do not occur on peromyscines. Except for the introduced *L. nuttalli*, the species were taken almost exclusively on *Oryzomys* and related complex-penis-type Cricetinae. The species of *Tur* occur almost entirely on caviomorph rodents of the family Echimyidae, of South American origin. *Mysolaelaps* also is neotropical and occurs on South American complex-penis-type cricetines and on caviomorphs. Two related genera, *Longolaelaps* and *Tricholaelaps* occur on Murinae (*Rattus*) in Sumatra.

Haemolaelaps is a cosmopolitan genus with more than 60 species which are associated with a wide range of hosts, but chiefly sciurumorph rodents (Tipton, op. cit., p. 242). *H. glasgowi*, the only species taken in Panama, occurred on a wide variety of small mammals, including rodents of the three suborders and marsupials (table 12).

The 14 described species of *Gigantolaelaps*, chiefly South American, are almost exclusively parasites of oryzomyine Cricetinae. The five species taken in Panama were originally described from South America; all have been taken in Venezuela, four of them also in Brazil, the fifth in Peru. All except one occurred below 5000 feet in Panama. *Gigantolaelaps inca*, described from Peru, was taken only above 5000 feet, chiefly on *Oryzomys*

albicularis and *O. alfaroi* (fig. 150) sparingly on *Peromyscus* and *Didelphis*.

The genus *Eubrachylaelaps* is closely related to *Haemolaelaps*, *Cavilaelaps* (on South American caviomorphs) and *Gigantolaelaps* (Furman, 1955; Tipton, op. cit.). The eight described species occur mostly on the simple-penis-type cricetines, *Peromyscus* and *Neotomodon*, in the subtropical and temperate altitudes and latitudes from Panama to California. *Eubrachylaelaps rotundus* Fonseca has been reported only from South America (Brazil and Venezuela) from a variety of sciuromorph and complex-penis-type myomorph (cricetine) rodents and marsupials. About half of the specimens taken in Venezuela (Furman and Tipton, 1961) were from *Zygodontomys*. This appears to represent a host transfer for *Eubrachylaelaps*.

The total numbers of Laelaptinae collected are tabulated for each genus of mites and of hosts, in table 12. We are aware that this method of presentation has many weaknesses, e.g., it does not show the host associations by species. Nonetheless it does show the preponderant associations of *Eubrachylaelaps* with *Peromyscus*, of *Gigantolaelaps* with complex-penis-type Cricetinae, especially *Oryzomys*; of *Laelaps* with caviomorph rodents and complex-penis-type Cricetinae; the promiscuity of *Haemolaelaps glasgowi*; the restriction of *Steptolaelaps* to the sciuromorph Heteromyidae, and of *Tur* to the caviomorph Echimyidae.

To summarize—of the eight genera that occur in Panama, three (*Laelaps*, *Haemolaelaps*, *Echinolaelaps*) are cosmopolitan; three (*Mysolaelaps*, *Gigantolaelaps*, *Tur*) are primarily South American, and are associated in Middle and North America with rodents of South American derivation or affinities; while *Eubrachylaelaps* and *Steptolaelaps* appear to be Middle and North American in origin.

The principal hosts of one South American genus (*Tur*) are caviomorph rodents. The principal hosts of the other two, as well as of two of the cosmopolitan genera, are primarily Murinae, and Microtinae, and complex-penis-type Cricetinae. Most Murinae and the Microtinae have complex penes, too. The occurrence of the preponderance of the Laelaptinae on rodents of this type suggests that Hershkovitz's treatment (1962) of the Cricetinae as a subfamily of the Muridae is sound. It is of special significance that many of the host associations of the genera of Laelaptinae are at a suprageneric level, as evidenced strikingly by the species of *Tur* on Echimyidae (Caviomorpha) and of the genus *Steptolaelaps* on Heteromyidae (Sciuromorpha). Thus, the differences in host associations between the related genera *Eubrachylaelaps* and *Gigantolaelaps*, with *Eubrachylaelaps* on simple-penis-type Cricetinae (Peromyscini, see Hooper and Musser, 1964, p. 54) and *Gigantolaelaps* only on complex-penis-type Cricetinae (chiefly oryzomyine genera) suggest a long period of geographic isolation and of differentiation of the two groups of hosts and parasites.

If we have belabored this point, it is because we believe it is important to establish the point—as evidenced by their mites and other ectoparasites, as well as by their distribution—that the simple-penis-type Cricetinae do appear to constitute a group, phyletically distinct from the other New World

TABLE 12. NUMBERS OF LAELAPTINE MITES COLLECTED IN PANAMA,
ACCORDING TO GENERA OF HOSTS AND MITES.
(introduced species not included)

Hosts	<i>Tur</i> (2 spp.)	<i>Myolaelaps</i> (<i>parvispinosus</i>)	<i>Echinolaelaps</i> (<i>lowei</i>)	<i>Laelaps</i> (3 spp.)	<i>Eubrachylaelaps</i> (<i>jamesoni</i>)	<i>Gigantolaelaps</i> (5 spp.)	<i>Steptolaelaps</i> (<i>heteromys</i>)	<i>Haemolaelaps</i> (<i>glasgowi</i>)	No. of host animals examined
Order MARSUPIALIA									
Family Didelphidae									
Philander (opossum)	8	109
Metachirus (nudicaudatus)	47	41
Didelphis (marsupialis)	10	..	3	207
Order RODENTIA									
Suborder Sciuromorpha									
Family Sciuridae									
Sciurus (<i>granatensis</i>)	26	129
Family Heteromyidae									
Liomys (<i>adpersus</i>)	4	3	62
Heteromys (2 spp.)	1	1	..	146	5	80
Suborder Myomorpha									
Family Cricetidae									
Subfamily Cricetinae									
* <i>Oryzomys</i> (10 spp.)	309	2	1928	..	89	296
* <i>Nectomys</i> (<i>alfari</i>)	2	28	..	11	3
* <i>Zygodontomys</i> (<i>microtinus</i>)	144	..	26	..	2	74
* <i>Sigmodon</i> (<i>hispidus</i>)	20	..	20	..	49	153
<i>Tylomys</i> (<i>panamensis</i>)	1	9
<i>Peromyscus</i> (2 spp.)	3	236	16	..	102	329
<i>Reithrodontomys</i> (3 spp.)	5	1	1	..	44	174
<i>Scotinomys</i> (2 spp.)	20	121
Suborder Caviomorpha									
Family Echimyidae									
<i>Proechimys</i> (<i>semispinosus</i>)	1610	35	..	1	..	9	616
<i>Hoplomys</i> (<i>gymnurus</i>)	18	5	9

* = Complex-penis-type Cricetinae.

Cricetinae, as postulated by Hooper (1960, p. 19).¹⁶ We believe that failure to recognize this distinction, has caused considerable confusion in thinking about the history and relationships of the Cricetinae and their parasites, and that it has led to erroneous conclusions regarding the immigration and evolution of the Cricetinae in South America.

B. Rove Beetles

Family Staphylinidae

Subfamily STAPHYLININAE. The distribution of the staphylinid beetles of the tribe Amblyopinini roughly parallels that of the stephanocircid fleas. These interesting beetles, which parasitize small mammals, are at present centered in South America. Seevers (1952) recognized five genera (table 13), one of them monotypic and known only from Tasmania where it occurs on a native murid. Three genera, with 19 species, are restricted to the South American continent; but *Amblyopinus*, with ± 30 species, is represented by five species in Panama, Guatemala, and Mexico. Amblyopinini are chiefly temperate in distribution, those of the middle latitudes being mostly montane. In South America they are largely restricted to the Patagonian Subregion, though a number of species occur in the southern part of the Brazilian Subregion, in the Andes of Colombia, and in the highlands of Venezuela and the Guianas. In Panama, they were taken at altitudes above 5000 feet; in Guatemala, above 6000 feet.

Seevers (op. cit.) regarded *Myotyphlus* from Tasmania as the most generalized genus and *Edrabius* of the Patagonian Subregion as most closely related and derived from the same stock. He considered the other three genera to have evolved from a common stock, with *Megamblyopinus*, *Amblyopinus*, and *Amblyopinodes* to be more specialized, in that order. *Edrabius* and *Megamblyopinus*, the most generalized South American genera are known only from *Ctenomys* (Caviomorpha) in the Patagonian Subregion. While most of the species of *Amblyopinus* appear to be host-species specific, the taxonomic range of hosts for the genus is considerable, and includes marsupials and various sciurormorph, caviormorph, and myomorph rodents.

Amblyopinodes, the most specialized genus, is confined mostly to South American complex-penis-type Cricetinae. Machado-Allison (1963) has shown that ten of the known species occur on *Akodon*, *Holochilus*, *Nectomys*, *Oryzomys* (2 species), *Oxymycterus* and *Scapteromys*; the eleventh species is from *Cavia*. He stated (op. cit., p. 414) that "parasitism [by *Amblyopinodes*] on *Oryzomys*, a genus of Holarctic [!] origin, and upon *Cavia* is secondary or accidental in the second case." There is no reason to believe that the association with *Oryzomys* is secondary. *Oryzomys* is related to *Nectomys*. Indeed, all of the hosts listed except *Cavia*, are South American complex-penis-type Cricetinae. Further, there is no reason to assume

¹⁶ Hooper stated that this group of genera "has the aspect of a distinct natural unit, of subfamily or family rank, which like the Heteromyidae and Geomyidae is endemic to the New World. The possibility that it is a natural group now requires intensive investigation, using all pertinent information." But, see also HersHKovitz (1966b).

TABLE 13. NUMBERS OF SPECIES OF AMBLYOPININE STAPHYLINID BEETLES BY GEOGRAPHIC AREA.

Genus	Total Species	S.A.	PAN.	GUAT.	MEX.	TAS.	Hosts
<i>Myotyphlus</i>	1	1	Myomorpha (Muridae)
<i>Edrabius</i>	6	6	Caviomorpha (<i>Ctenomys</i>)
<i>Megamblyopinus</i>	2	2	Caviomorpha (<i>Ctenomys</i>)
<i>Amblyopinus</i>	±30	26	2	1	2	..	Marsupialia Rodentia: Caviomorpha, Sciuromorpha, Myomorpha
<i>Amblyopinodes</i>	11	11	Myomorpha (S.Am. Cricetinae) Caviomorpha (<i>Cavia</i>)

(S.A. = South America; PAN. = Panama; GUAT. = Guatemala; MEX. = Mexico; TAS. = Tasmania).

that *Oryzomys* is of holarctic origin in any different sense than might be postulated for all the other South American Cricetinae.

It is noteworthy that *Amblyopinus*, the only genus with Middle American representatives, is also the only one which exhibits marked ecological polyvalence, as indicated by both its host and geographic distribution in South America. The Middle American species appear to have transferred to peromyscine Cricetinae and to parasitize them almost exclusively. This may reflect the relative lack of complex-penis-type hosts in the montane zones. It is most interesting that *Amblyopinodes*, whose species are restricted to *Oryzomys* and other complex-penis-type Cricetinae, has not been found in Middle America.

C. Batflies

Family Streblidae

Of the 23 described genera of New World Streblidae, 20 are known from Panama, and two others almost certainly occur there. Two monotypic genera *Eldunnia* (*breviceps*) and *Parastrebla* (*handleyi*), are known only from Panama. Since their hosts are primarily South American in distribution, these flies probably occur there too. One genus, *Joblingia*, is known only from the montane zones of Panama (Chiriquí), Costa Rica, and Guatemala, and is probably endemic to the warm temperate areas of Middle America.

All of the other genera that occur in Middle America and the Antilles also occur in South America, as do most of the species. In northern Mexico

and southwestern United States, there are a few species that do not occur in either Panama or South America, and also one group—the *Trichobius major* group—from which *Joblingia* and *Anatrichobius* were almost certainly derived. The most generalized representatives of this group, *T. major*, *corynorhini*, and *hirsutulus*, occur on Vespertilionidae in southern United States, Mexico, the highlands of Guatemala, and in the Greater Antilles. Somewhat more specialized species occur in the Greater Antilles (on Vespertilionidae); the most specialized ones occur on other hosts, including Chilonycterinae, both in the Greater Antilles and in Middle America. One, *T. sparsus*, occurs in the lowlands of Panama, on *Pteronotus parnellii fuscus* (Phyllostomidae: Chilonycterinae).

Two described genera are known only from South America, but probably only one (*Synthesiostrebla*) is restricted to that continent. An undescribed genus has been taken from *Noctilio l. leporinus*¹⁷ in Surinam, northern Brazil (near Surinam) and Venezuela. The *Trichobius pallidus* group (which is closely related to the *caecus* group), is known to us only from the two genera of Furipteridae. The *caecus* group occurs on the related family Natalidae and the apparently related Chilonycterinae (see Wenzel, Tipton, and Kiewlicz, this volume, pp. 443–4, 447–8, 652–3).

Two genera that appear to be centered in South America, extend into Panama. They are *Pseudostrebla*, on species of *Tonatia* in the lowlands, and *Anatrichobius*, on *Myotis* in the lower montane zone.

The only endemic genera and species groups in Middle America, then, are primarily temperate or subtropical in distribution, with a few derived species in the tropical lowlands. One other genus and one species group could be regarded as centered in, though not restricted to the West Indies, southwestern United States, and Middle America. These are *Nycterophilia* and the *Trichobius caecus* group, whose principal and probably original hosts appear to be Natalidae and Chilonycterinae. The Chilonycterinae and Natalidae occur in the Antilles and in Middle and South America. We are not in a position to judge at this time whether this distribution represents a recent dispersal or is a fairly old one. It is old enough for speciation to have occurred in both of the major geographic areas concerned. If the dispersal is a recent one from Middle America and the Greater Antilles to South America, these hosts and their streblids might be part of an earlier endemic tropical lowland fauna that was isolated until the emergence of the Panama land bridge. However, judging from their distribution in the Greater Antilles, dispersal of these hosts was probably not unduly hampered by relatively narrow water gaps. The only Streblidae for which the Panamanian isthmus seems to have been a barrier, either with or without water gaps, are temperate forms like *Joblingia*.

The lowland tropical Streblidae of Middle America and the coastal lowlands of Colombia, Peru, and Western Venezuela, form a faunal unit. It is replaced by an "allopatric" unit in eastern Venezuela, the Guianas, and

¹⁷ It has not been taken from the races of *Noctilio leporinus* that occur in the Amazon basin, northwest South America and Middle America, or the Greater Antilles.

parts of the Amazon Basin; this in turn is replaced by other faunal assemblages in various parts of the Amazon Basin and southern South America.

To summarize, the tropical lowland streblid fauna of Panama is exceptionally rich and representative and is entirely a continuation of the South America fauna. Because few Streblidae are temperate, the montane fauna is very limited. The few clearly endemic Middle American elements occur entirely in the montane zones. These are chiefly species and species groups, although there is one endemic genus, *Joblingia*. Panama appears to be the southern limit of this genus, and is the most northern limit known of the related genus, *Anatrichobius*, whose principal distribution is in the highlands and southern latitudes of South America. There are no taxa of Streblidae common to the New and Old Worlds. Dispersal between the two was probably very early.

Family Nycteribiidae

Of 13 genera of Nycteribiidae, only two are known from the New World. *Herskovitzia*, the most generalized genus of the family, is known from two species that parasitize the highly specialized, ecologically isolated, relict family Thyropteridae in South America. Since *Thyroptera* occurs in Panama, *Herskovitzia* may ultimately be found there, too. The other nycteribiid genus, *Basilia*, occurs in both the Old and the New World, chiefly on Vespertilionidae. Since the principal host genus, *Myotis*, occurs in both hemispheres, one is tempted to conclude that the entire dispersal is recent. However, as pointed out by Guimarães and D'Andretta (1956), there are distinctive endemic elements of the genus in Middle and South America whose distributions suggests that there was an earlier dispersal, too. This is also suggested by the occurrence on *Myotis* of Streblidae of the *Trichobius major* group and of the genera *Joblingia* and *Anatrichobius*. These appear to have evolved on *Myotis*, yet have no Old World relatives.

All of the Nycteribiidae that are known from Panama occur in the lowland tropics. As pointed out by Guimarães (p. 402, this volume), "Panamanian Nycteribiids seem to belong to the South American assemblage of *Basilia* species."

E. Fleas

The two preceding groups are primarily tropical and subtropical in distribution. Their distributions exhibit many features in common with those of the fleas, though the latter are primarily temperate in distribution and show numerous relationships with Old World forms. In the following discussion we have treated those forms whose host and geographic distributions have a bearing on the faunal relationships of the native fleas of Middle and South America. Table 17 should be consulted for a summary of the numbers of genera and species of native New World fleas according to families and geographic subregions. Figure 149 shows the altitudinal distribution of the Panamanian fleas. We have drawn heavily upon Johnson (1957) for information regarding South American fleas, and upon Hopkins and Rothschild (1953, 1956, 1962) for information regarding certain families of Middle and North American fleas. For a comprehensive review of

host associations of fleas, for the world, refer to Hopkins (1957a).

Family Pulicidae

Subfamily TUNGINAE (including Hectopsyllinae). These are largely confined to South America. *Tunga penetrans* has been carried by man to other tropical parts of the world, and two species have been described from China.¹⁸ Of the five South American species of *Tunga*, four are restricted to Southern Brazil, while the fifth, *T. penetrans*, occurs throughout the tropical lowlands of South and Middle America. Its dispersal within the hemisphere may have been facilitated by man.

The genus *Hectopsylla* is centered in the Patagonian Subregion, with eight species described from South America, chiefly from birds and caviomorph rodents. None have been taken in Panama, but *H. knighti* Traub is known from Mexico. This is one of the few genera of primarily temperate South American distribution that is found in the montane zones of Middle America. The fact that the species of this genus infest birds probably explains its dispersal across the isthmus.

The two species of the genus *Rhynchopsyllus* parasitize bats of the genus *Molossus* (Molossidae). One species is known from Peru and Panama, the other from numerous localities throughout South America, chiefly in the southern latitudes and interior Peru, Ecuador, Colombia, and (?) Venezuela.

Subfamily PULICINAE. Tribe Pulicini. Of the genus *Pulex*, only the human flea, *P. irritans*, has been recorded from South America. The four other known species occur in Middle America and the United States. *Juxtapulex echidnophagoides*, is known from Panama and Costa Rica. In Panama, its principal hosts appear to be the armadillo, *Dasypus novemcinctus fenestratus* and the opossum, *Didelphis marsupialis cauae*.

Tribe Spilopsyllini. *Actenopsylla* with a single species (*suavis*) of bird flea is known only from Mexico. All of the other native species of Pulicidae that have been taken in Middle and South America, are rabbit fleas of the genera *Hoplopsyllus* (subg. *Euhoplopsyllus*) and *Cediopsylla*. These are two of the only flea genera of recent holarctic or nearctic derivation that occur in South America. The genus *Cediopsylla* has not been taken in Panama. One species, *spillmanni* Jordan, has been taken in Peru, and the two North American species have been taken in Mexico. The genus is restricted to the western hemisphere.

The genus *Hoplopsyllus* is represented north of Mexico by four species, one of the subgenus *Hoplopsyllus* and three of *Euhoplopsyllus*. *Hoplopsyllus* (*E.*) *glacialis* is widespread, with three subspecies in the New World, one each in Turkestan and China and one in Panama. *Hoplopsyllus g. exoticus*

¹⁸ It has been suggested (Hopkins, 1957a, p. 79) that the occurrence of *T. caecigena* in China represents an introduction from South America. The recent description of a second species (*callida*) from Yunnan, China makes this appear dubious. A similar distribution is known for the Histeridae (Coleoptera). The senior author recently received an undescribed species of *Binhister*, collected in Santa Catharina, Brazil, by Fritz Plau-mann. The described species are from Japan and Indo-China.

is the only representative of the genus that has been taken in Panama (above 5000 feet, fig. 149). It has not been recorded from South America. The two species of *Euhoplopsyllus*—*manconis* Jordan from Ecuador and Peru, and *andensis* from Peru—that are known only from South America may be subspecies of *H. (E.) glacialis* (Johnson, 1957; Hopkins and Rothschild, 1953).

Family Malacopsyllidae

This family contains two monotypic genera, *Malacopsylla* and *Phthiropsylla*, both endemic to Argentina. The principal records of both are from edentates and carnivores. The family is almost certainly relict.

Family Rhopalopsyllidae

This family is related to the Malacopsyllidae. The species are restricted to the New World, with the exception of some species of *Parapsyllus*. The Parapsyllini with 42 species and subspecies in eight genera, occur chiefly in the Patagonian Subregion at southern latitudes or high elevations. Their principal host associations are with cricetine and caviomorph rodents, with one genus, *Parapsyllus*, on penguins in South America, in the Falklands, South African coastal islands, other southern hemisphere islands, and Australia. None of this tribe have been taken north of Ecuador.

The Rhopalopsyllini include 54 species and subspecies in three genera in South America. The six species of the genus *Tiamastus* are confined to the Patagonian Subregion, where they occur chiefly on caviomorph rodents. There are a few records from complex-penis-type Cricetinae. The other two genera, *Rhopalopsyllus* and *Polygenis*, include many species that are montane in distribution. They also include a larger number of warm-adapted species, than do most other South American flea genera. Of 41 species of fleas recorded from Brazil (chiefly southern), 26 belonged to these two genera. This climatological range is also reflected in the altitudinal distribution of species taken in Panama (fig. 149).

All of the Rhopalopsyllini taken in Panama also occur in South America (!), with the possible exception of *Rhopalopsyllus* sp. near *mesus*. Johnson (1957) recognized four subspecies of *Rhopalopsyllus australis*: *R. a. tupinus*, recorded from Panama, Peru, Bolivia, and Brazil; the nominate subspecies described from Mexico and possibly restricted to Middle America; the other two subspecies occurring only in South America.

The host records of *Rhopalopsyllus* are not adequate to establish the principal hosts of most South American species. They appear to be primarily parasites of caviomorph rodents, and edentates, and perhaps to a lesser extent their predators, and some marsupials. The number of specimens taken from various hosts in Panama is shown in table 14. In Panama, *R. a. tupinus* is clearly a characteristic parasite of *Dasyprocta punctata*, and to a lesser extent of *Nasua nasua* and *Tayassu tajacu*; *R. cacicus saevus* is a parasite of *Dasypus novemcinctus*; and *R. l. lugubris* is a parasite of *Agouti paca* and, at higher elevations, of *Dasyprocta punctata* as well—in place of *R. cacicus saevus*!

TABLE 14. NUMBERS OF FLEAS OF THE GENUS *RHOPALOPSYLLUS* TAKEN IN PANAMA, ACCORDING TO SPECIES OF NATIVE MAMMAL HOSTS.†

Hosts	<i>R. australis</i> <i>tupinus</i>	<i>R. cacticus</i> <i>saevus</i>	<i>R. lugubris</i> <i>lugubris</i>	<i>R. lugubris</i> <i>cryptoctenes</i>
Order MARSUPIALIA				
Family Didelphidae				
<i>Philander opossum</i> (109)	1
<i>Metachirus nudicaudatus</i> (41)	..	1
<i>Didelphis marsupialis</i> (207)	7	18	10	..
<i>Chironectes minimus</i> (2)	6
Order EDENTATA				
<i>Tamandua tetradactyla</i> (7)	4
<i>Dasybus novemcinctus</i> (20)	..	181
Burrows (<i>Dasybus</i>) (20)	..	254
Order RODENTIA				
Family Sciuridae				
<i>Sciurus granatensis</i> (129)	1
Family Cricetidae				
<i>Zygodontomys microtinus</i> (74)	2
Family Dasypodidae				
<i>Agouti paca</i> (13)	19	1	32	115
<i>Dasypoda punctata</i> (35)	226	2	4	36
Family Echimyidae				
<i>Proechimys semispinosus</i> (616)	14	5
Order CARNIVORA				
Family Procyonidae				
<i>Nasua nasua</i> (27)	63	2
<i>Galictis allamandi</i> (1)	1
Order ARTIODACTYLA				
Family Tayassuidae				
<i>Tayassu tajacu</i> (1)	30

† numbers in parentheses following hosts = numbers of specimens examined.

The species of *Polygenis* are found on a wide variety of hosts in South America, but the principal associations appear to be with complex-penis-type Cricetinae, and to a lesser extent with caviomorph and other rodents. In Panama, most specimens of *P. atopus* were from *Peromyscus n. nudipes*, but the small numbers taken suggest that this is probably not the principal host. The principal host associations of the other three species (table 15) were as follows: *P. dunni* with *Liomys adspersus* (Heteromyidae); *P. klagesi*

TABLE 15. NUMBERS OF FLEAS OF THE GENUS *POLYGENIS* TAKEN IN PANAMA, ACCORDING TO SPECIES OF NATIVE MAMMAL HOSTS.†

Hosts	<i>P. atopus</i>	<i>P. dunni</i>	<i>P. klagesi</i>	<i>P. r. beebei</i>
Order MARSUPIALIA				
Family Didelphidae				
<i>Marmosa robinsoni</i> (108)	3	3
<i>Philander opossum</i> (109)	3
<i>Metachirus nudicaudatus</i> (41)	..	2	..	1
<i>Didelphis marsupialis</i> (207)	10	10
Order RODENTIA				
Suborder Sciuromorpha				
Family Sciuridae				
<i>Sciurus granatensis</i> (129)	..	1	..	1
Family Heteromyidae				
<i>Liomys adspersus</i> (62)	..	38	2	..
Suborder Myomorpha				
Family Heteromyidae				
<i>Heteromys australis</i> (21)	1	..
" <i>desmarestianus</i> (80)	1
Family Cricetidae				
Subfamily Cricetinae				
* <i>Oryzomys albigularis</i> (25)	1
* " <i>bombycinus</i> (7)	2	10
* " <i>caliginosus</i> (94)	43
* " <i>capito</i> (100)	..	1	4	49
* <i>Nectomys alfari</i> (3)	6
* <i>Zygodontomys microtinus</i> (74)	..	2	11	3
* <i>Sigmodon hispidus</i> (153)	..	1	1	..
<i>Tylomys panamensis</i> (9)	31	..
<i>Peromyscus nudipes</i> (322)	1
Family Erethizontidae				
<i>Coendou mexicanus</i> (5)	33	..
Family Dasyproctidae				
<i>Dasyprocta punctata</i> (35)	4	..
Suborder Caviomorpha				
Family Echimyidae				
<i>Proechimys semispinosus</i> (616)	..	3	2313	4
<i>Hoplomys gymnurus</i> (9)	81	..
Order CARNIVORA				
Family Procyonidae				
<i>Nasua nasua</i> (27)	43	..

† numbers in parentheses following hosts = numbers of host specimens examined.

* = complex-penis-type Cricetinae.

probably with *Proechimys* (Echimyidae); and *P. roberti beebei* with *Oryzomys* (Cricetinae). Most other associations of the Middle and North American species appear to be with *Oryzomys* and *Sigmodon*, though one species, *P. floridanus* (Florida), appears to have transferred to *Peromyscus*. The association of *P. klagesi* with *Liomys* is not quantitatively established. The relatively small numbers of *P. dunni* collected, and the small percentage of *Liomys* found parasitized (17.7%) suggest that *Liomys* may not be the principal host. The few available records suggest that in South America it is *Sigmodon hispidus* (the type host, from Panama). However, of 153 specimens of this host that were examined in Panama, only one was positive for this flea.

It seems reasonably clear from the geographic and host distribution records that the species of *Rhopalopsyllus* are recent arrivals from South America. In the case of *Polygenis* it appears that this genus has been present in Middle and North America long enough for endemic species and species groups to develop. Hershkovitz has indicated (p. 735, this volume) that species of the *Oryzomys palustris* complex and of the *Sigmodon hispidus* complex are Middle American descendants of the earliest cricetine invaders from South America. If this is so, then it is quite likely that the invading hosts carried fleas of the genus *Polygenis* with them into Middle America, and that this partly explains the endemism found in this genus north of Panama.

Thus, most species of *Rhopalopsyllus* belong to Hershkovitz's (op. cit.) Stratum III and the endemic Middle American species of *Polygenis* to his Stratum IV.

Family Ceratophyllidae

This family is primarily holarctic in distribution. The genera of Ceratophyllidae that occur in Panama are *Dasypsyllus*, *Pleochaetis*, *Kohlsia*, *Jellisonia*, and *Ceratophyllus*. The first three are the only genera of Ceratophyllidae, other than introductions, that have been taken in South America.

The species of *Dasypsyllus* are parasites of birds. The genus is widely distributed in the temperate latitudes and altitudes. Seven species are reported from the New World. *Dasypsyllus gallinulae perpinnatus* occurs along the coast of western North America to Panama. Specimens of *gallinulae* have been recorded from Venezuela and Argentina, but have not been identified to subspecies (Johnson, 1957). The nominate subspecies occurs in western Europe. *Dasypsyllus stejnegeri* has been reported from Siberia and the Pribiloff Islands; it has also been taken in Mexico (unpublished record, Traub, pers. comm.) and the Falkland Islands. The other five New World species are South American (chiefly Patagonian); but *Dasypsyllus lasius* is represented by the subspecies *venezuelensis* in montane Venezuela and Panama.

About 17 species of *Ceratophyllus* are known from the New World, 16 from the United States and Canada. One (*gallinae*) was introduced from Europe. Two species have been reported from Mexico, and one (*C. altus*) from the upper montane zone of Panama (fig. 149). None have been reported from South America.

TABLE 16. HOST ASSOCIATIONS OF FIVE MIDDLE AMERICAN GENERA OF FLEAS AS SHOWN BY NUMBERS COLLECTED IN PANAMA, ACCORDING TO GENERA OF NATIVE HOSTS.

Hosts	No. of hosts examined	<i>Kohlsia</i> (6 spp.)	<i>Jellisonia</i> (2 spp.)	<i>Pleochaetis</i> (2 spp.)	<i>Strepsylla</i> (<i>dalmati</i>)	<i>Wenzella</i> (<i>yunker</i> i)
Order RODENTIA						
Suborder Sciuromorpha						
Family Sciuridae						
<i>Sciurus</i> (2 spp.)	129	20	..	245†	3	..
Family Heteromyidae						
<i>Heteromys</i> (<i>desmarestianus</i>)	80	1	..	1	..	59
Suborder Myomorpha						
Family Cricetidae						
Subfamily Cricetinae						
* <i>Oryzomys</i> (3 spp.)	296	14	1	20
* <i>Nyctomys</i> (<i>sumichrasti</i>)	4	..	3
<i>Peromyscus</i> (2 spp.)	329	409	9	122	14	..
<i>Scotinomys</i> (2 spp.)	38	3	45	41	5	..
<i>Reithrodontomys</i> (3 spp.)	107	1	3	96	8	..

* = complex-penis-type Cricetinae. † = *Pleochaetis d. dolens*.

The remaining genera—*Pleochaetis*, *Jellisonia* and *Kohlsia*—are of special interest, because they appear to be primarily temperate genera which are restricted to or centered in the highlands of Middle America, chiefly on *Peromyscus* and related simple-penis-type Cricetinae and tree squirrels of the genus *Sciurus*. Their host associations are shown in table 16.

Only two species of the genus *Pleochaetis* are recorded from the (south-western) United States. One of these, *P. sibynus*, also occurs in Mexico. The other is a subspecies of *P. equatoris*, a species of unusually wide distribution. The nominate form occurs from Peru and Ecuador to Mexico, though it was not taken in Panama. *Pleochaetis dolens* is known from Ecuador (*P. d. quitanus*) and Panama to Mexico (*P. d. dolens*). The only other species known from Panama is *P. altmani*. It was taken chiefly from species of *Reithrodontomys*, *Scotinomys xerampelinus*, and *Peromyscus n. nudipes*, while *P. dolens dolens* was taken chiefly from *Sciurus granatensis chiriquensis* and *Peromyscus nudipes nudipes*, with scattered records from other hosts. The other Middle American species have been taken chiefly from *Peromyscus*. Two species are known only from South America, *P. smiti* and *P. apollinaris*, both from Colombia. They have been taken from various hosts, chiefly complex-penis-type Cricetinae.

With a single exception, the 17 species of the genus *Kohlsia* are limited to Middle America. Six species have been recorded from Panama, only one from South America. This latter species, *K. campaniger* was taken from "*Hesperomys*" sp. in Ecuador. Its generic assignment is doubtful (Traub, 1952). The species of *Kohlsia* appear to be parasites chiefly of *Peromyscus* and other simple-penis-type Cricetinae and of *Sciurus*. Of the Panamanian species, *K. azuerensis* was taken from *Peromyscus flavidus*; *K. graphis graphis* was taken only from *Sciurus granatensis chiriquensis*; of 18 specimens of *keenani*, eight were from simple-penis-type cricetine rodents (*Peromyscus* and *Scotinomys*) and ten from complex-penis-type cricetines (*Oryzomys*);¹⁹ *K. mojica* is known only from *Peromyscus n. nudipes*; *K. tiptoni* from *Sciurus granatensis chiriquensis*; *traubi* chiefly from *Peromyscus n. nudipes*, with scattered records from other hosts.

There are ten known species of *Jellisonia*. Nine have been reported from Mexico; of these, *ironsi* Eads and *bullisi* Traub and Johnson have also been taken in southwestern United States. *Jellisonia johnsonae* is known only from Panama. The genus has not been reported from South America. Most of the species have been taken from *Peromyscus* and related genera of simple-penis-type cricetine rodents, like *Baiomys* and *Reithrodontomys*, but one has been taken from *Microtus* (Microtinae) according to Traub (1952).

Family Ischnopsyllidae

Six genera of bat fleas have been reported from the New World. Three of these (*Hormopsylla*, *Ptilopsylla*, and *Rothschildopsylla*) are known only from the tropical lowlands. *Rothschildopsylla* is known only from South America. Three species of *Hormopsylla* are known from South America, and one (*kyriophila*) from Panama. They are parasites of molossid bats, as is true of the two species of *Ptilopsylla*, *dunni* from Panama and *leptina* from Brazil. The genus *Sternopsylla* is obviously South American in its relationships. The single species is closely related to those of the preceding two genera (Hopkins and Rothschild, 1956) and like them occurs on molossid bats. It is represented by the subspecies *S. distincta texana* in the United States and Mexico, *S. distincta speciosa* in Panama and Peru, *S. d. distincta* in Paraguay and Parana, Brazil. *Sternopsylla d. speciosa* was taken in the lower montane zone in Panama (fig. 149). The three genera of bat fleas that have been taken in Panama thus appear to be South American in their relationships.

Myodopsylla and *Nycteridopsylla*, the other two genera that occur in the New World, are holarctic. *Nycteridopsylla* does not occur in Middle or South America. The North American *Myodopsylla collinsi* has been taken as far south as Chocoyos (Dept. of Chimaltenango) Guatemala, in the montane zone. Three species of *Myodopsylla* have been described from

¹⁹ The few species of *Oryzomys* that were parasitized by them had such a scattered representation of flea species, that none can be regarded as characteristic hosts for these fleas.

South America, but none have been reported from between Guatemala and Colombia. The species of both genera parasitize vespertilionid bats of the genus *Myotis*. It seems likely that a species of *Myodopsylla* may be found in the highlands of Panama. The distribution pattern of this genus in the New World somewhat parallels that of certain nycteribiid batflies of the genus *Basilia*, which also occurs chiefly on *Myotis*.

Family Pygiopsyllidae

This family is known from the Australian, Oriental, Palaearctic (one species), Ethiopian and Neotropical Regions. Three subfamilies are recognized, two with only one genus each, the third (Pygiopsyllinae) with ± 15 genera. Only the Pygiopsyllinae are represented in the New World, by one genus, *Ctenidiosomus*. The three described species are mostly from complex-penis-type cricetine rodents (*Oryzomys*, *Thomasomys*, *Rhipidomys*, *Neomys*). They are montane (Andean) in distribution, with species from Peru, Ecuador and Colombia. Undescribed species are known from South America. One has recently been collected in Costa Rica (det. Traub; Truxal, pers. comm.)! It was not taken in Panama, though it may occur there.

Family Hystrichopsyllidae

The Hystrichopsyllidae occur chiefly in the Holarctic Region. At first glance, it might appear that the South American forms represent a recent intrusion of northern hemisphere groups into South America. An analysis of the distributions and relationships does not support this. The South American representatives belong to three subfamilies, as follows:

Subfamily HYSTRICHOPSYLLINAE. *Ctenoparia* is the only genus of the tribe Ctenopariini. The two known species occur on complex-penis-type cricetine rodents in Chile and Argentina.

Subfamily CTENOPHTHALMINAE. No representatives of this subfamily have been taken in Middle America, except *Ctenophthalmus*. There are three genera in South America: *Chiliopsylla* (*allophylla* Rothsch.), whose host is dubious; *Neotyphloceras*, with two species that occur almost exclusively on complex-penis-type cricetine rodents in Argentina and in the Andes north to Colombia; and *Agastopsylla*, with six species all in the Patagonian Subregion, at high elevations or far southern latitudes, chiefly on complex-penis-type cricetines. *Chiliopsylla* and *Neotyphloceras* are the only genera of the tribe Neotyphloceratini, while *Agastopsylla* is the only genus of the tribe Agastopsyllini. The distribution and taxonomic position of these genera, including those whose species are on cricetines suggest a considerable period of isolation in South America.

Subfamily DORATOPSYLLINAE. Smit (1962) lists six genera, representing four tribes: the Idillini, with a single genus *Idilla* from marsupials in Australia; the Acedestini, with a single monotypic genus *Acedestia* from marsupials in Australia; Tritopsyllini, with a single genus *Adoratopsylla*, from marsupials in South and Middle America; and Doratopsyllini with *Doratopsylla*, *Corrodopsylla*, and *Xenodaeria* from insectivores. *Xenodaeria* is known only from Sikkim. The holarctic *Doratopsylla* and *Corrodopsylla* occur on shrews. The southernmost record of these is a species of *Corrodop-*

sylla from Guerrero, Mexico (Traub, pers. comm.). No fleas of this genus were found on the four specimens of the shrew *Cryptotis* sp. examined in Panama.

Three species of the subgenus *Adoratopsylla* have been taken on South American marsupials, mostly at southern latitudes in Brazil and at intermediate elevations in Venezuela and Colombia. The single species of the subgenus *Tritopsylla* is represented in South America by four subspecies, one of which, *A. (T.) intermedia copha*, occurs in Panama. A fifth subspecies has been taken in Mexico.

We have dwelt at some length on these doratopsylline fleas because *Doratopsylla* and *Adoratopsylla* have been considered to be very closely related genera, and it seemed that the occurrence of *Adoratopsylla* on marsupials might represent a recent host divergence from the Holarctic *Doratopsylla*. But, as pointed out by Smit (op. cit.), the geographic and host distributions of the genera of Doratopsyllinae and the tribal allocations of the genera suggest that the host associations of these fleas are very old. Thus the occurrence of *Adoratopsylla* in Middle America most likely represents an intrusion from South America.

Subfamily NEOPSYLLINAE. None of the genera of this subfamily have been taken in South America. Only two genera have been reported from Middle America: a species of *Meringis* from Mexico and seven species of *Strepsylla*, six of them from Mexico and one from Panama. The species of *Strepsylla* are montane and occur chiefly on species of the genus *Peromyscus* and related simple-penis-type Cricetinae. The genus appears to be endemic to Middle America.

Subfamily RHADINOPSYLLINAE. This holarctic subfamily is not represented in South America. The genus *Wenzella*, which represents a taxonomically isolated tribe (Traub, 1953; Hopkins and Rothschild, 1962), is known from only two species, *W. obscura* Traub from Guatemala and *yunkeri* n.sp. from Panama. Both were taken at altitudes above 6000 feet on *Heteromys desmarestianus* (Heteromyidae). The genus appears to be an old endemic of the Middle American highlands. The Heteromyidae, too, are primarily Middle American in distribution.

Family Stephanocircidae

Two subfamilies are recognized. The Stephanocircinae include a single genus (*Stephanocircus*) with five species, all from Australia and Tasmania, and occurring chiefly on marsupials, but also on *Rattus*. The Craneopsyllinae, with seven genera and 27 described species are known only from South America, with the exception of *Plocopsylla scotinomi* from Panama. Nearly all of them are from the Patagonian Subregion. Many are found at elevations of 10,000 to 16,000 feet in Peru.²⁰

Although the species of *Plocopsylla* parasitize caviomorph and myo-

²⁰ Because of distinctive conditions in Peru, temperatures at these high altitudes are more comparable to those at lower altitudes in Panama.

morph rodents and marsupials in South America, they appear to occur most frequently on complex-penis-type Cricetinae. The principal host of *P. scotinomi* was clearly *Scotinomys teguina*, a simple-penis-type cricetine. This probably represents a host transfer, similar to that undergone by the species of *Amblyopinus* (rove beetles) in Middle America.

Summary

Perhaps the most notable feature of the flea fauna of Panama (and all Middle America) is that there are no endemic tropical lowland genera. The tropical-subtropical lowland fauna is with few exceptions, predominantly South American, much of it probably of recent origin. Most of it has close relationships—even to the subspecies level—with coastal Colombia, Ecuador, and Peru. Above 5000 feet the fauna is largely Middle and North American or Holarctic in its relationships, but, excluding introduced species, it has few genera in common with the fauna north of Mexico, except for species that occur on ubiquitous or highly vagile hosts, like some bats, rabbits, and birds.

Of the 25 species taken above 5000 feet (fig. 149) 13 (52%) belong to genera that are known only from or are largely centered in Middle America: *Pulex*, *Juxtapulex*, *Strepsylla*, *Wenzella*, *Kohlsia*, *Pleochaetis*, and *Jellisonia*. Of 16 species that were taken *only* above 5000 feet, the percentage was considerably higher (approx. 69%). Two others were obviously of northern origin (*Hoplopsyllus glacialis* and *Ceratophyllus altus*). The main point illustrated by these data is that in Middle America there are a number of genera that are endemic or nearly so and nearly all are found at higher altitudes and/or northern latitudes, and chiefly on host genera that are restricted (or nearly so) to Middle and North America.

Of the 18 species that were restricted to the montane zones, or nearly so, only five can be regarded as South American derivatives. They are *Polygenis atopus*, *Rhopalopsyllus l. cryptoctenes*, *Sternopsylla speciosa* (bats), *Dasyopsyllus l. venezuelensis* (birds), and *Plocopsylla scotinomi*. Two others, which occur in Middle America but were not taken in Panama, are *Hectopsylla knighti* (birds) from Mexico and *Ctenidiosomus* sp. from Costa Rica. With the exception of *Plocopsylla*, none of the South American genera occurred above 6000 feet in Panama. Only three species of Middle or North American genera occurred below 4000 feet, *none* below 2000 feet.

No endemic genera of close South American relationships are known to occur in the montane zones of Panama or elsewhere in Middle America. The converse is true of South America.

The fleas of South America like those elsewhere, are primarily temperate in distribution. Thus, in South America they occur chiefly in the Patagonian Subregion and in the cordilleras. With the exception of a few obviously recent arrivals, a few highly vagile forms, and some introductions, the fauna consists chiefly of endemics or of groups, like the Rhopalopsyllidae, which are predominantly centered in South America but may have dispersed outward. Among these latter are cold temperate forms like *Parapsyllus* (penguin fleas), or genera with warm-adapted species like *Rhopalopsyllus* and *Polygenis*, which occur in Middle and North America, chiefly on hosts of

South American origin. Only a very few temperate South American forms like some bird fleas (e.g., *Dasyopsyllus lasius*) and *Plocopsylla scotinomi* and *Ctenidiosomus* sp. occur in Middle America. The relationships of the South American fleas are chiefly with the southern hemisphere of the Old World, especially with the Australian Region, but also with the Ethiopian and Oriental Regions. A few South American genera like *Ctenoparia* and *Adoratopsylla* belong to hystrichopsyllid groups like the Hystrichopsyllinae and Doratopsyllinae which are predominantly Holarctic. However, these genera belong to endemic tribes and are probably relicts.

Very few representatives of the Middle American fauna have penetrated South America, except a few species of *Pleochaetis*, and possibly *Kohlsia* and a few other recent invaders like *Cediopsylla* and *Euhoplopsyllus*, on such vagile hosts as rabbits and possibly squirrels. Since 1), there are no endemic tropical lowland genera in Middle America; 2), the native lowland fleas are overwhelmingly South American or of South American affinities, and 3), there are very few representatives of Middle and North American genera in South America, then it appears that recent dispersals of small mammals and their fleas have been predominantly from South into Middle America rather than the converse. An earlier (perhaps pre-Pleistocene) dispersal may account for endemic species of *Rhopalopsyllus* and *Polygenis* in Middle America.

Very few montane forms appear to have moved in either direction across the isthmus. We believe that dispersal across the "bridge" by some of these temperate genera²¹ may have been facilitated by lower temperatures than exist at present (see Nygren, 1950; Dorf, 1959, map 5). This may well have been one of the principal factors which permitted dispersal of many forms between the two continents, rather than the elevation of the Bolivar trough.

VII. Zoogeographic Conclusions

With the exception of some conspicuously recent immigrants²² into South America from Middle America, the distribution patterns shown by the ectoparasites hold true for most of the hosts, too. It is especially striking in the case of the cricetine rodents, those of the montane region being largely simple penis types (Peromyscini), which have barely penetrated South America, while cricetine hosts of the lowland subtropical zones are largely complex penis types of South American relationships, e.g., *Oryzomys*, *Sigmodon*, and *Zygodontomys*.

Among the ectoparasites, we have found little evidence of endemism in the tropical lowlands of Middle America, except north of Panama, and there, entirely at the species level. It is significant that nearly all of the lowland parasites belong to: 1), genera which otherwise occur only in the lowland

²¹ For example, such South American genera as *Ctenidiosomus* and *Plocopsylla* (fleas) and *Amblyopinus* (staphylinid beetles), and Middle American genera like *Pleochaetis* and *Kohlsia* (fleas).

²² Like rabbits, some squirrels, cats, deer, shrews, spiny mice (*Heteromys*), camels, bears, etc.

tropics of South America, e.g., the bat fleas *Hormopsylla*, *Ptilopsylla*, and *Rhynchopsyllus*; or 2), "expanding" South American genera, like *Polygenis* and *Rhopalopsyllus*, which on that continent have both temperate and warm-adapted species.

We do find ample evidence in the fleas, mites, and Streblidae, of the existence of a distinctive Middle American ectoparasite fauna, but in the subtropical and especially the temperate altitudes and latitudes. It is characterized by the flea genera *Pleochaetis*, *Kohlsia*, *Jellisonia*, *Wenzella*, *Strepsylla*, and probably *Juxtapulex*; by the streblid genus *Joblingia* and the generalized members of the *Trichobius major* group; and by laelaptid mites of the genera *Steptolaelaps* and *Eubrachylaelaps*. Deserts may have isolated many of these genera from North America (north of Mexico) and they may also have been a barrier to the southward dispersal into Mexico of more recent northern temperate groups. They appear to have been more effective barriers for non-host-limited parasites than for their hosts or than for host-limited parasites, probably because of the narrower climatic tolerances of the non-host-limited forms.

What is especially interesting is that these Middle American groups of ectoparasites are largely restricted to simple-penis-type cricetine rodents, especially *Peromyscus*, *Reithrodontomys*, and *Scotinomys* in Panama, as well as other genera like *Baiomys* and *Neotomodon* farther north. These hosts, too, are primarily temperate (altitudinally and latitudinally) in distribution.

These distribution patterns suggest that the tropical lowland fauna has probably moved between Panama and South America with relative ease, for a considerable time. On the other hand, the fauna of the subtropical and temperate (montane) zones of Middle America shows an increasing degree of endemism, and thus of isolation from South America, the higher the altitudes. This suggests that the extensive "sea" of lowland tropical rain forests in Panama, especially in the Darién, may have been more effective in isolating the distinctive temperate Middle and South American ectoparasites and their hosts than was the waterway between Panama and South America (the Bolivar Portal). Portals and lowlands north of the Isthmus of Panama probably also served as isolating barriers, but we are not concerned with them in this discussion.

It is difficult to reconcile these conclusions with the view of Simpson (1950) and Patterson (1957) that the ancestors of the complex-penis-type South American Cricetinae immigrated into South America over a land bridge which arose in the Pliocene-Pleistocene, and subsequently: 1), evolved into an array of 50 genera and ± 300 species; 2), acquired a considerable

Table 17. Explanation of abbreviations.

AUS. = Australian region; M.AM. = Middle America; COS. = Cosmopolitan; ETH. = Ethiopian region; HOL. = Holarctic Region; N.AM. = North America, north of Mexico; NE. = Nearctic Subregion; NW. = New World; OR. = Oriental Region; PAL. = Palaearctic Subregion; PAN. = Panama; S.AM. = South America; SO. ISLDS. = Islands of the Southern hemisphere.

Table 17. Numbers of Genera (bold face) and Species (roman) of Native Fleas in South, Middle, and North America, according to Family.

	S.A.M.	PAN.	MEX.	M.A.M.	N.A.M.	Distribution
Pulicidae						
TUNGINAE	3/14	2/2	2/2	3/3	..	NEO., PAL.
PULICINAE						
Pulicini	..	2/3	2/5	2/5	2/2	M.A.M., HOL., ETH., AUS.
Spilopsyllini	2/3	1/1	2/4	2/4	2/6	HOL., NEO.
Malacopsyllidae	2/2	S.A.M.
Rhopalopsyllidae						
RHOPALOPSYLLINAE						
Parapsyllini	8/39	S.A.M., AUS., & SO. ISLDS.
Rhopalopsyllini	3/38	2/7	2/3	2/11	1/2	NEO., NE.
Ceratophyllidae						
CERATOPHYLLINAE	4/12	5/12	13/43	13/54	17/111	HOL., ETH., OR., NEO.
FOXELLIINAE	2/5	2/5	2/18	NE.
Leptopsyllidae						
AMPHIPSYLLINAE	5/6	HOL.
Ischnopsyllidae	5/9	3/3	2/2	3/4	3/8	COS.
Vermipsyllidae	1/5	HOL.
Pygiopsyllidae	1/3	1/1	..	AUS., OR., ETH., NEO.
Hystrichopsyllidae						
HYSTRICHOPSYLLINAE						
Hystrichopsyllini	2/3	2/3	2/7	HOL.
Ctenopariini	1/2	S.A.M.
STENOPONIINAE	1/1	1/1	1/2	HOL.
NEOPSYLLINAE						
Neopsyllini	1/1	1/1	2/2	HOL., OR.
Phalacropsyllini	..	1/1	2/7	2/6	5/38	HOL.
ANOMIOPSYLLINAE						
Jordanopsyllini	1/1	NE.
Anomiopsyllini	5/26	HOL.
RHADINOPSYLLINAE						
Corypsyllini	2/10	NE.
Rhadinopsyllini	1/1	1/1	3/11	HOL.
Wenzellini	..	1/1	..	1/2	..	M.A.M.
DORATOPSYLLINAE						
Doratopsyllini	1/1	1/1	2/5	HOL.
Tritopsyllini	1/5	1/1	1/1	1/1	..	NEO.
CTENOPHTHALMINAE						
Ctenophthalmini	1/4	1/4	1/1	HOL.
Carterettini	1/2	NE.
Neotyphloceratini	2/3	S.A.M.
Agastopsyllini	1/4	S.A.M.
Stephanocircidae						AUS., NEO.
CRANEOPSYLLINAE	7/26	1/1	NEO.

fauna of South American ectoparasites; 3), moved back (*Oryzomys*, *Sigmodon*, etc.) into Middle and North America with their newly acquired parasites, where 4), they were isolated long enough to differentiate (as did their parasites) into species that are distinct from the South American ones now inhabiting the lowlands in Panama and elsewhere in Middle America.

With very few exceptions, the ectoparasites of these complex-penis-type cricetine rodents belong to families and tribes or genera which are either restricted to or centered in South America, and whose closest relatives are in most cases Old World forms, especially of the Australian Region, but also of the Oriental and (to a much lesser extent) Ethiopian Regions. Only a very few parasites that are identifiable as Middle or North American, and these are obviously fairly recent intruders, occur on these hosts. Among these are the laelapine mite *Eubrachyla elaps*, a few fleas of the genus *Pleochaetis*, another of the genus *Kohlsia*,²³ and several rabbit fleas of the genera *Cediopsylla* and *Hoplopsyllus* (Subg. *Euhoplopsyllus*). The geographic and host distributions of lice like *Hoplopleura*, cited by Vanzolini and Guimarães (1955), must be re-examined.

The complex-penis-type Cricetinae, like *Oryzomys* and *Sigmodon*, that occur north of Panama, can hardly be relicts of an old fauna that dispersed into South America, if their fleas (*Polygenis*) are an indication. *Polygenis* is an "expanding" South American genus which has, quite clearly, dispersed into Middle America along with complex-penis-type Cricetinae and caviomorph rodents from South America. Most of the Panamanian species probably dispersed very recently. In most cases they are not even subspecifically distinct from South American forms.

Further, there seems to be little other reason to accept the Pliocene-Pleistocene transition as the principal time of dispersal²⁴ of the ancestral complex-penis-type cricetine rodents (and possibly some other mammals, too) into South America. Even if the fossil Cricetinae known from the Upper Pliocene of the Argentine (see following paper) reflect the first appearance of these rodents in southern South America, this may mark the end of a long "trail" of dispersal and evolution rather than the beginning (see Hershkovitz, pp. 727-732).

Because the implications of our distributional data appeared to conflict with prevailing views regarding the dispersal of the Cricetinae into South America, we discussed the problem with Mr. Philip Hershkovitz. His account of their origin, dispersal and radiation (see following paper) generally agrees with our conclusions regarding the ectoparasites.

Acknowledgments

We wish to express our gratitude to the following persons for reading

²³ Many of the Ceratophyllidae are squirrel fleas (Hopkins 1957a). This is true of some species of *Pleochaetis* and *Kohlsia*, too. The few South American species of these genera may have immigrated on squirrels.

²⁴ It is important to note that Nygren (1950, p. 2005. See also following paper by Hershkovitz, this volume, p. 725) believes that the Panama land bridge may have been available for passage by terrestrial animals since the close of the Middle Miocene!

portions of the manuscript and offering suggestions and corrections: Mr. Henry Dybas of Chicago Natural History Museum, for reading the section of the manuscript relating to coexistence and competitive displacement; Profs. Alfred E. Emerson and Lynn Throckmorton, of the Department of Zoology, of the University of Chicago, for reading the section on host specificity; Col. Robert Traub, U. S. Army (Ret.), School of Medicine, the University of Maryland, for reading the entire manuscript, and especially the portions dealing with the fleas; and, Mr. Philip HersHKovitz, Chicago Natural History Museum, for reading the entire paper as it relates to mammal hosts. The geologic history, zoogeography and ecology of the cricetine hosts have been discussed at length with Mr. HersHKovitz.

Abstract

The authors discuss host specificity, coexistence and competitive displacement, altitudinal distribution, some epidemiological considerations, and faunal relationships and their zoogeographic implications. The need for new approaches to field sampling and analysis of host and ectoparasite populations is emphasized.

It is suggested that the degree of host-parasite specificity in ectoparasites is largely correlated with the degree to which the parasite is host-limited, i.e., restricted to the host, during its life cycle. Thus, a high degree of host specificity occurs most commonly among hemimetabolous groups whose life cycle is spent on the host; among holometabolous forms whose free-living early stages have been eliminated through ovoviviparity and thus remain closely associated with the host most of the time; or holometabolous forms which are closely confined with the host by the physical nature of its "home", as e.g., in kangaroo rat burrows, pocket gopher burrows, etc. It is further suggested that in host-limited forms, homozygosity for host specificity is achieved quickly, and likewise, speciation and niche specialization, because of inbreeding. This is in contrast with the situation in those ectoparasites which are non-host-limited, like most fleas and heteroxenous ticks, in which there is extensive outbreeding. It is further suggested that polyhaematophagy is selected for in these non-host-limited forms. In such non-host-limited forms either a broadly adaptive genetic variability or balanced polymorphism as regards host specificity would greatly increase the chances of host-finding and thus of survival.

A case of coexistence and possible competitive displacement among streblid batflies parasitic on *Phyllostomus hastatus* is discussed. The data indicate that the altitudinal distribution of host-limited forms parallels that of the hosts closely, while there is a notable lack of concordance between that of non-host-limited parasites and their hosts.

The altitudinal distributions of the ectoparasites when correlated with their systematics and geographic and host relationships indicate that: 1), the tropical lowland faunae of Panama and northern South America are virtually identical, but endemism increases correspondingly with increase in altitude, and is marked in the temperate zones, both altitudinally and latitudinally; 2), this is largely true of the lowlands north of Panama, too, but here species endemism is evident; 3), the temperate (including the montane) fauna of South America is largely precinctive with considerable endemism at the family, subfamily and tribal level, and is Old World, especially Southern Hemisphere in its relationships; 4), the montane fauna of Middle America likewise shows considerable endemism, but chiefly at the generic level, and its relationships are overwhelmingly with the Holarctic Region; 5), very little interchange is evident between the temperate faunae of the two continents, excepting parasites of such vagile hosts as birds, bats, and squirrels; 6), recent dispersals of ectoparasites of small mammal hosts, especially Cricetinae, appear to have been chiefly from South to Middle, rather than from Middle to South America. The data appear to conflict with the views of Simpson (1950) and Patterson (1957, fig. 9), regarding the dispersal and radiation of the Cricetinae in South America, during the Pliocene-Pleistocene. It is suggested that dispersal of these rodents into South America took place in the Miocene or earlier.

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